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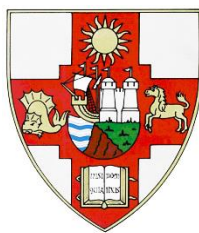
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Spatial ecology and conservation management of the endangered sandhill dunnart, *Sminthopsis psammophila*

Joanna Louise Riley

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of PhD in the Faculty of Life Sciences.



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Abstract

We are experiencing a global biodiversity and climate crisis that is rapidly causing the extinction of species. Mammal species have been disproportionately affected; however, this trend is considerably worse in Australia. Since Australia's occupation by Europeans, 34 mammal species have been declared extinct. Australian mammals in deserts are particularly at risk of extinction. Many arid zone mammals have specialised adaptations to their hostile, unpredictable ecosystems. For example, they use thermally insulative refuges, prefer habitats that reduce predation risk, or have large home ranges and broad diets to maximise energy intake. Understanding these adaptations is essential for informed conservation management. However, little ecological data is known for the sandhill dunnart, *Sminthopsis psammophila*, an endangered and charismatic marsupial that now remains within just a few natural refugial habitats in Australia's southern deserts. To address conservation biology knowledge gaps, an integrated, evidence-based approach (i) quantified the diurnal and nocturnal ecology of *S. psammophila* in the Western Australian Great Victoria Desert (WAGVD), (ii) estimated the past, present and future distributions of *S. psammophila* throughout Australia, (iii) examined the key threats to *S. psammophila* - particularly wildfires and anthropogenic climate change - and (iv) proposed conservation management solutions for a) *S. psammophila* and b) sympatric arid zone species. Between 2015 and 2019, radio tracking and global positioning system (GPS) technologies examined the sheltering, foraging, dietary and habitat preferences of *S. psammophila* in the WAGVD. In contrast to its previously reported habitat preferences, *S. psammophila* preferred burrowing within long unburned (32+ years since a wildfire) spinifex (*Triodia* spp.) grassland habitats. Dense lower stratum swale, sand plain and dune slope habitats were preferred, whereas habitats lacking spinifex and open dune crest habitats were rarely used. Hence, wildfires were identified as a significant threat to the species.

The sheltering preferences of *S. psammophila* agreed with the premise that small desert mammals often use shelters with thermal advantages and anti-predation benefits, such as burrows, *Lepidobolus deserti* hummocks and logs. Conversely, spinifex hummocks were not found to be insulative against extreme temperatures and were not preferred. The foraging adaptations of *S. psammophila* agreed with the premise that arid zone species often have large home ranges to exploit resource patches or islands. The 100 % home ranges of *S. psammophila* [mean: 70 ha; range: 6-274 ha; minimum convex polygon (MCP)] were influenced by sex and reproductive status. In addition, a Formicine-rich diet indicated that ants are an important dietary resource for *S. psammophila*. Species distribution models (SDMs) predicted the past, present, and future distributions of *S. psammophila*, evaluated the environmental parameters that determine the species' distribution and identified habitats of high conservation value. The past model supported evidence that *S. psammophila* was widespread but has recently contracted to more climatically favourable areas of its geographic range. Ground-validation of the present model's predictions discovered a population 150 km north of the species' known range. Future models identified that climate change is a potential catastrophic threat for *S. psammophila*. By 2050, under Representative Concentration Pathway (RCP) 8.5 (our current pathway) there is a predicted 95 % reduction in suitable habitat for *S. psammophila* in the WAGVD. By 2070 (RCP 8.5), only the Eyre Peninsula population may remain viable and the continental distribution of *S. psammophila* may contract by up to 80 %. However, this contraction is predicted to be halved if global greenhouse gas emissions peak in 2040 then reduce (RCP 4.5). Due to specific habitat preferences for long unburned habitats, *S. psammophila* is further restricted within its climatically and geographically suitable range. As a semi-arid specialist, it is also vulnerable to drought-related population crashes. Hence, *S. psammophila* should remain listed as endangered at the state and federal level, and its status should be revised by the International Union for Conservation of Nature.

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Jo Riley, Jeff Turpin, David, Ramona and Chris Riley, Jeff, Mike Griffiths, Jeff and Jo



Brynne Jayatilaka, Peter Turpin, Jeff, Rose Lane and Zac Simms



Gareth Jones, Ray Lloyd, Carly Watson, Jeff, Jo, Chris, Matt Zeale and Belinda Bastow

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such below. Any views expressed in the dissertation are those of the author.

Tracking was performed by Joanna Riley with assistance from Jeff Turpin, Ray Lloyd, Carly Watson, Zac Sims, Peter Turpin, Brynne Jayatilaka, Genevieve Alderson, Nitin from APA, and Isobel Sewell. This project was performed in conjunction with the 'Sandhill Dunnart Monitoring Program' for APA and Kingfisher Environmental Consulting. APA supplied research funding for tracking and TGM provided invaluable in-kind field support. Ground-validation was funded by the GEMG. Additional camera trap data were collated with permission from surveys performed by Kingfisher Environmental Consulting for APA and the Great Victoria Desert Biodiversity Trust (GVDBT). Motion cameras were donated by Kathryn Sinclair (GVDBT), Dr Judy Dunlop at the Department of Biodiversity, Conservation and Attractions (DBCA), Ray Lloyd (FaunaTrack) and Mike Griffiths. Dr Brian Heterick performed morphological faecal pellet analyses and identified invertebrates in the field. Dr Alex Baynes confirmed historical *S. psammophila* records in Western Australia.

Joanna Louise Riley

Signed:

Date:

Table of Contents

Abstract	i
Acknowledgements.....	iii
Author's declaration	vi
Table of Contents	vii
List of Tables and Figures.....	xi
Chapter 1: General Introduction	1
1.1. Global conservation biology issues	2
1.2. Integrated and evidence based conservation biology	4
1.3. Desert ecology and survival	5
1.4. Australia as a world leader in mammal extinctions	8
1.5. The Great Victoria Desert study site	19
1.6. Carnivorous marsupials and the Dasyuridae.....	25
1.7. The sandhill dunnart, <i>Sminthopsis psammophila</i> : background information and knowledge gaps.....	27
1.8. Thesis Outline.....	42
Chapter 2: Shelter types and habitat preferences	46
Abstract	47
2.1. Introduction	48
2.2. Methods.....	54
2.2.1. Study site	54
2.2.2. Trapping, tagging and tracking protocol.....	55
2.2.3. Shelter habitat analyses	56
2.2.4. Statistical analyses.....	59
2.3. Results.....	61
2.3.1. Site level.....	61
2.3.2. Shelter plot characteristics	63
2.3.3. Generalised linear mixed effects models (GLMMs) for shelter and random plots	65
2.3.4. Shelter types selected by <i>S. psammophila</i>	66
2.3.5. Shelter use.....	68
2.3.6. Temperature recordings	69
2.4. Discussion	75
2.4.1. Overview	75
2.4.2. Shelter selection of <i>S. psammophila</i>	75

2.4.3. The sheltering adaptations of sympatric arid zone mammals	79
2.4.4. Limitations.....	81
2.4.5. Conservation management	82
2.4.6. Summary	83
Chapter 3: Foraging, ants, and islands - the nocturnal ecology of <i>S. psammophila</i>	85
Abstract.....	86
3.1. Introduction.....	87
3.2. Methods	95
3.2.1. Study site	95
3.2.2. Trapping, tagging and habitat preferences	95
3.2.3. Dietary preferences.....	99
3.2.4. Statistical methods	100
3.3. Results	102
3.3.1. Ranging behaviour of <i>S. psammophila</i>	102
3.3.2. Weather and moon phase results	106
3.3.3. Phuassess: habitat use of <i>S. psammophila</i>	106
3.3.4. Habitat densities, number of shrubs and floristic richness	108
3.3.5. Dietary preferences.....	109
3.4. Discussion.....	113
3.4.1. Overview.....	113
3.4.2. The nocturnal ranging behaviour of <i>S. psammophila</i>	114
3.4.3. The dietary preferences of <i>S. psammophila</i>	120
3.4.4. Limitations.....	122
3.4.5. Conservation management	123
3.4.6. Summary	125
Chapter 4: MaxEnt species distribution models (SDMs) and ground-validation of model predictions in Western Australia	127
Abstract.....	128
4.1. Introduction.....	129
4.2. Methods	132
4.2.1. Study site	132
4.2.2. Occurrence records	132
4.2.3. MaxEnt SDM procedure.....	133
4.2.4. Ground-validation methods	135

4.2.5. Confusion matrix and threshold-dependent analysis	136
4.3. Results.....	136
4.3.1. Model predictions	136
4.3.2. Environmental variables	137
4.3.3. Ground-validation of the MaxEnt SDM	139
4.4. Discussion	141
4.4.1. Overview	141
4.4.2. Environmental variables and climate	142
4.4.3. Detection improvements.....	142
4.4.4. Limitations	143
4.4.5. Conservation management	143
4.4.6. Summary.....	146
Chapter 5: Climate change and conservation planning.....	148
Abstract	149
5.1. Introduction.....	150
5.2. Methods.....	153
5.2.1. Study site and species.....	153
5.2.2. Modelling procedure	154
5.2.3. Statistical analyses.....	156
5.3. Results.....	156
5.3.1. Summary.....	156
5.3.2. Statistical interpretation	160
5.4. Discussion	161
5.4.1. Overview	161
5.4.2. Environmental variables and <i>S. psammophila</i> ecology	162
5.4.3. The mid-Holocene past model and recent contractions	163
5.4.4. Important pressures that may affect the future distribution of <i>S.</i> <i>psammophila</i>	165
5.4.5. Limitations	166
5.4.6. Conservation management	166
5.4.7. Summary.....	168
Chapter 6: General Discussion.....	170
6.1. Overview.....	171
6.2. Habitat preferences and small desert mammals	171
6.3. Foraging behaviour, ranging and diet.....	174

6.4. Species distribution models, climate change and conservation status assessments	178
6.5. Limitations	181
6.6. Future applications and suggestions for arid zone management	183
6.7. Closing remarks	186
References.....	187
Appendices.....	241

List of Tables and Figures

Figure 1-1. Sketches from the Horn Expedition.....	10
Figure 1-2. The cumulative number of extinct mammal taxa in Australia.....	12
Figure 1-3. <i>Sminthopsis psammophila</i> captures and annual rainfall.....	17
Figure 1-4. The Western Australian Great Victoria Desert (WAGVD) study site.....	19
Figure 1-5. Habitat photographs in the WAGVD	22
Table 1-1. Habitat class descriptions and proportions available	23
Figure 1-6. A structural cross section of habitat classes within the WAGVD	24
Figure 1-7. The endangered sandhill dunnart, <i>Sminthopsis psammophila</i>	27
Figure 1-8. Historical occurrence records of <i>S. psammophila</i>	34
Figure 1-9. The life cycle of ring-forming spinifex hummocks	37
Figure 2-1. Diurnal tracking sites within the study site.....	55
Figure 2-2. The number of shelters within each habitat class.....	62
Table 2-1. Bonferroni's confidence intervals	63
Figure 2-3. Shelter and random habitat plot densities	63
Figure 2-4. Mean distance to dune crest.....	64
Table 2-2. List of habitat variables from the best generalised linear mixed effects models (GLMMs) at the plot level	65
Table 2-3. The top five most parsimonious and best fitting GLMMs	66
Figure 2-5. The mean number of shelter days each shelter type was used.....	69
Figure 2-7. Photographs of the shelter types of <i>S. psammophila</i>	71
Table 2-4. Shelter selection of <i>S. psammophila</i>	72
Table 2-5. Daily temperature recordings within diurnal shelters	73
Table 2-6. Daily temperature recordings within shelter habitat classes	74
Figure 3-1. Examples of 100 % minimum convex polygon (MCP) home range areas and 90 % cluster core areas	96
Figure 3-2. The utilisation distribution discontinuity (UDD) analysis	98
Figure 3-3. All 100 % minimum convex polygon (MCP) home range areas.....	103
Table 3-1. The ranging behaviour of <i>S. psammophila</i>	104
Table 3-2. 100 % MCP home range area, 90 % cluster core area and maximum range span linear mixed effects models (LME) models	105
Table 3-3. Most parsimonious and best fitting LME models	106
Table 3-4. Phuassess simplified ranking matrix	107
Table 3-5. Habitat densities in the nocturnal foraging range of <i>S. psammophila</i> ...	108
Figure 3-5. The number of shrubs and overall species richness	109
Figure 3-6. <i>Sminthopsis</i> spp. dietary preferences	110

Figure 3-7. Non-metric multidimensional scaling (NMDS) of <i>Sminthopsis</i> spp. dietary composition	111
Figure 3-8. The habitat classes used by <i>S. psammophila</i> during foraging	112
Table 4-1. The final environmental variables used to predict the distribution of <i>S. psammophila</i> throughout Australia in 2016.....	133
Figure 4-1. Motion-sensing camera trap locations in Western Australia.....	135
Figure 4-2. The binary MaxEnt species distribution model for <i>S. psammophila</i>	137
Figure 4-3. Threshold-independent statistical output	138
Figure 4-4. Ground-validated <i>S. psammophila</i> presences in the WAGVD	139
Figure 4-5. Examples of ground-validation images of <i>S. psammophila</i>	140
Table 4-2. A confusion matrix	140
Figure 4-6. Threshold-dependent results.....	141
Figure 4-7. Long unburned and suitable habitat for <i>S. psammophila</i>	144
Figure 4-8. Cumulative fire scar area by year	145
Table 5-1. All bioclimatic data and general circulation models	153
Table 5-2. The final environmental variables used for climate change modelling..	155
Figure 5-1. Past, present and future predictions of the climatically and geographically suitable distribution for <i>S. psammophila</i>	158
Figure 5-2. The binary past, present and future models for <i>S. psammophila</i>	159
Figure 5-3. Threshold-independent statistical output	160
Figure 5-4. Historical mean temperature anomaly in Australia.....	161
Figure 5-5. Historical climate data from Kalgoorlie-Boulder weather station	165
Table 5-3. Area of preferred habitat and total population declines from present to future under a range of climate change scenarios	168
Figure 6-1. Burned sheltering habitat of <i>S. psammophila</i>	173
Figure 6-2. Surplus killing of a radio tracked <i>S. psammophila</i> by a feral cat	175
Figure 6-3. Large wildfires, droughts and hot winds in the WAGVD.....	182
Figure 6-5. Threatened mammal species activity in the Australian arid zone has rapidly declined due to droughts.....	185
Appendix A. Site locations and descriptions for radio and GPS tracked <i>S. psammophila</i> in the WAGVD	241
Appendix B. Morphometric, reproductive and tracking data for nocturnally tracked individuals	242
Appendix C. All prey items recorded in the diet of <i>S. psammophila</i>	244
Appendix D. <i>Sminthopsis psammophila</i> records used for SDMs	246

Chapter 1: General Introduction



1.1. Global conservation biology issues

We are experiencing a global biodiversity crisis with species' extinctions now occurring at approximately 1000 times the predicted background rate (Ceballos *et al.* 2010, Butchart *et al.* 2010, Pimm *et al.* 2014, IPBES 2019). Most global extinctions are related to habitat loss/fragmentation caused by prolific human population growth (Hoffmann *et al.* 2010, Dirzo *et al.* 2012). Other anthropogenic extinction drivers include climate change, agricultural expansion and pesticides, logging, environmental mismanagement, pollution and overexploitation, over-hunting/fishing, and the introduction of invasive species (Dexter *et al.* 1995, Hooper *et al.* 2012, Hoffmann *et al.* 2019). A lack of government action to save species - particularly in Australia - is a further challenge (Woinarski *et al.* 2017, 2019a, Wintle *et al.* 2019). Mammal species are particularly vulnerable to extinction and approximately one quarter of all global mammal species are threatened (Ceballos and Ehrlich 2002, Johnson 2006, Hoffmann *et al.* 2011, IUCN 2020). The extinction of mammal species can have significant trophic consequences as many perform essential ecosystem functions such as controlling overgrazing by herbivores, e.g., wolves, *Canis lupus*, in Yellowstone National Park (Laundré *et al.* 2001), or habitat engineering, e.g., pika, *Ochotona pallasii*, in Mongolia which influence soil nutrient levels by burrowing (Wesche *et al.* 2007). However, the increasing rate of extinction conceals the impact of conservation successes (Garnett *et al.* 2018a), without global conservation efforts there would be significantly more extinctions today (Hoffmann *et al.* 2010) and an optimistic attitude toward conservation can yield significant results (Clark *et al.* 1994, Balmford 2012).

The field of conservation biology was inspired by the observations of early naturalists, e.g., Finlayson (1936, 1958, 1961) in central Australia, and evidence of Earth's vanishing biodiversity due to environmental mismanagement, e.g., 'Silent Spring' by Rachel Carson (1962). The central aim of conservation biology is to provide a legitimate scientific basis to preserve biological diversity, maintain functioning

ecosystems and to generate answers when scientific knowledge is lacking (Soulé 1985, Robinson 2006, Van Dyke 2008). First, we must understand the biology of a rare and/or threatened target species and its importance within its ecosystem (Brussard 1991). Key methods include investigating the evolutionary perspective, community ecology, population viability, autecology, reproduction, distribution and range contraction, genetic structure, threats, diseases and natural history of a threatened species/ecosystem; this is accomplished by testing environmental hypotheses, improving human engagement with threatened species/ecosystems and by establishing environmental protection policies (Brussard 1991, Robinson 2006).

It can be challenging to monitor every aspect of biodiversity, particularly within remote regions such as arid Australia. Hence, several surrogate methods for single species conservation biology have been proposed that survey and/or conserve a single species to protect the biodiversity of an entire ecosystem (Simberloff 1998, Hilty and Merenlender 2000, Roberge *et al.* 2004, Caro 2010). It is far easier to measure the rate of decline of a single species rather than attempting to monitor an entire ecosystem with many species (Wilson 2016). For example, an indicator species indicates the 'health' of an ecosystem (Landres *et al.* 1988). An umbrella species protects large areas of natural habitat; hence, its conservation automatically saves many species within its range (Meffe and Carroll 1997, Simberloff 1998, Barua 2011). A flagship species is a charismatic species that elicits increased financial support thus protecting less fiscally popular species (Meffe and Carroll 1997, Ducarme *et al.* 2013) or is a leading symbol that can ignite public engagement, but a flagship need not necessarily be a good indicator or umbrella (Simberloff 1998). This thesis aims to provide evidence that the sandhill dunnart, *Sminthopsis psammophila*, may be considered all three of the above types of surrogate species. Thus, its conservation will identify pristine habitats, protect species within its range, generate financial support and improve public engagement using its appeal as an attractive animal.

1.2. Integrated and evidence based conservation biology

Integrated conservation biology is an approach that is beneficial for rare and/or threatened species as it uses multiple scientific methods, for example, conservation genetics to identify isolated populations with on-ground spatial ecology research (Zeale *et al.* 2012), thus, facilitating more informed recovery programs, establishing prioritisation and improving conservation strategies (Coates and Atkins 2001). In the integrated approach, autecological methods can be used to evaluate a threatened species' ecological requirements. Individuals within a population are studied to determine species-specific adaptations such as habitat preferences, environmental responses, movement, dietary preferences, survival adaptations or reproductive strategy (Walter and Hengeveld 2014). Spatial ecology methods using radio tracking and lightweight global positioning system (GPS) technologies are useful for autecological studies, and now enable the research of small, remotely located species (Aebischer *et al.* 1993, Tomkiewicz *et al.* 2010). In addition, predictive species distribution models (SDMs) can be used to improve survey methods, detect populations of a threatened species, monitor shifting distributions or to assess a species' extinction risk from climate change (Thomas *et al.* 2004, Rodríguez *et al.* 2007, Bellard *et al.* 2012). Evidence-based survey and conservation programs must then protect and monitor threatened populations to prevent future extinctions (Sutherland *et al.* 2004). Unfortunately, some conservation practice is based upon anecdotal myths rather than a systematic assessment of evidence, and is influenced by others who previously tackled the same problem (Sutherland *et al.* 2004) - this is particularly relevant for the conservation of *S. psammophila*, an elusive desert dwelling marsupial with few empirical studies.

1.3. Desert ecology and survival

Defining deserts can be challenging as there are many exceptions. However, Earth's deserts are most commonly defined as unpredictable, hostile landscapes with low productivity where little precipitation occurs and evaporation is too high to allow many species to survive (Shreve 1942, Thornthwaite 1948, Meigs 1953, Williams 2014).

Deserts are located from subtropical to polar regions, and are further characterised by extreme aridity, extreme fluctuations in ambient temperatures, windy conditions and solar radiation that is greater than evapotranspiration (UNEP 1992). Approximately one-third of the Earth's land surface is classified as either arid (80-350 mm annual rainfall) or semi-arid (200-500 mm annual rainfall) desert (UNESCO 1977).

Despite harsh environmental conditions, deserts are incredibly diverse ecosystems with flora and fauna species that have specialised physiological, morphological and/or behavioural adaptations, such as the ability to prevent overheating/overcooling, conserve water or maintain body temperatures at lower basal metabolic rates (McNab and Morrison 1963, Downs and Perrin 1990, Kinlaw 1999, Scott 2000, Schwimmer and Haim 2009, Degen 2012). Small desert mammals in particular are characterised by low evaporative water loss compared with mesic (non-desert) species, and use a variety of strategies for survival, without which, their relatively large surface area to body mass ratio would quickly cause lethal dehydration (Degen 2012). Many xeric (desert) fauna species are successful due to their nocturnal or crepuscular activity and the utilisation of thermally advantageous subterranean shelters during the day (Degen 2012). For example, cracking clay soils are exploited by the South American pallid fat-tailed opossum, *Thylamys pallidior*, and several Australian marsupial species (Pavey *et al.* 2014, Waudby and Petit 2017, Baker and Dickman 2018). In North America, kangaroo rats, *Dipodomys* spp., spend most of their lives underground within burrows that are so well constructed that the occupants have survived nuclear bomb testing in Nevada (Anderson and Allred 1964). Diurnally active desert fauna are less common but have

adaptations such as gaping their mouths and fluttering their throats [e.g., nomadic desert birds (Dean 2004)], estivation [e.g., the Mohave ground squirrel, *Citellus mohavensis* (Bartholomew and Hudson 1960)], thermoregulatory licking and the utilisation of shade [e.g., the Macropodidae (Dawson 1977)]. 'Shuttling' or the intermittent use of subterranean structures during the extreme heat of the day is used by many desert mammals, e.g., a species of Thar Desert gerbil, *Meriones hurrianae*, develops hyperthermia due to sun exposure but intermittently visits cool burrow systems to unload excessive heat (Prakash 1997) and rattlesnakes, *Crotalus* spp., in the Sonoran desert prevent overheating by sheltering within rock crevices (Beck 1995). Conversely, many diurnally active desert mammals such as rock hyrax, *Procavia capensis*, rest for up to 95 % of the day, have strong social groups and use sun basking (passive rewarming) for thermoregulation in cooler temperatures (Rübsamen *et al.* 1982). Physiological adaptations to conserve energy and water include prolonged dormancy during periods of aridity with response to large rainfall events [e.g., desert dwelling frogs, *Scaphiopus couchi* (Lee and Mercer 1967), *Neobatrachus* spp. and *Cyclorana* spp. (Withers 1995)], while others enter daily torpor - a controlled reduction in body temperature and basal metabolic rate that enables survival (Bozinovic and Marquet 1991, Geiser and Ruf 1995, Degen 2012).

Dietary and/or foraging adaptations of desert fauna species include 'optimal foraging' (Cowie 1977, Brown *et al.* 1999) to maximise their energy intake (e.g., Kotler and Brown 1999) and the efficient use of habitat to avoid predation risk (Verdolin 2006, Laundré *et al.* 2010, Bleicher and Dickman 2020). Foraging adaptations include caching food by herbivorous species (Randall 1993), flexible diets allow for exploitation of temporally and spatially variable resources (Morton *et al.* 1983), large home ranges that maximise unpredictable resource patches (Dickman *et al.* 1995, Letnic 2001, Baker and Dickman 2018), extracting preformed water from food (Kam and Degen 1993) and retaining dietary water by producing concentrated urine. For example, the

South American fat-tailed opossum, *Thylamys pusillus*, produces urine that is so highly concentrated it has burned through the clothes of researchers (Baker and Dickman 2018).

As resources are scarce and reproduction is costly, many desert flora and fauna species reproduce rapidly or “boom and bust” in response to favourable rainfall pulses that increase primary resources (Chesson *et al.* 2004, Letnic and Dickman 2006, Dickman *et al.* 2010, Thibault *et al.* 2010). Consequently, following rainfall events in deserts, wildfires are more prolific due to the accumulation of plant biomass, which plays an important role in establishing heterogenous habitat mosaics throughout the world (Minnich 1983, Haydon *et al.* 2000, Smit *et al.* 2013). As heterogenous habitats (habitat mosaics) with differing structural densities, vegetation richness or seral stages are critical for native mammal species richness worldwide (Kerr and Packer 1997, Letnic 2001, Holland *et al.* 2007, Bird *et al.* 2008), and invasive species such as the house mouse, *Mus domesticus*, and the feral cat, *Felis catus*, prefer disturbed vegetation (Holland *et al.* 2007, McGregor *et al.* 2015, 2017), the protection and restoration of heterogenous mosaics of landscapes in deserts is a global conservation priority. The habitat preferences of small arid zone mammals are often selected to facilitate their survival. For example, in a Brazilian temperate desert, the gray leaf-eared mouse, *Graomys griseoflavus*, selects vegetation patches with a greater quantity of preferred prey species, avoids open habitats, selects habitats with a greater flora species richness and prefers habitats with an increased density of lower stratum (grasses) and upper stratum canopy (Spirito *et al.* 2017).

The key threats to global desert ecosystems are anthropogenic. For example, urbanisation and industry increasingly encroach upon arid habitats, irresponsible tourism and habitat pollution/misuse causes direct environmental damage, soil erosion/salinization, overgrazing and nutrient depletion are caused by agriculture, introduced species alter habitats and prey upon or compete with native species, and,

climate change is causing increasingly severe and frequent droughts and wildfires in arid regions (Scott 2000, Martín-Queller *et al.* 2010, IPCC 2014, Brito *et al.* 2014, Doherty *et al.* 2015a, Afefe *et al.* 2016, CSIRO 2017).

Australia's deserts account for nearly 11 % of Earth's arid land surfaces (Meigs 1953, UNESCO 1977). Australian deserts are second in aridity only to the cold deserts of Antarctica and cover approximately 70 % of the continent (UNEP 1992, Beard 2014). The main factors causing aridity in Australia are its location at the southern end of the Hadley Cell - a zone of dry descending air (Diaz and Bradley 2004), the Eastern Highlands rain shadow, distance inland and the cold ocean current off the Western Australian coast (Williams 2014). Many aspects of desert ecology in Australia are poorly known and climate change is predicted to severely affect Australia in the future (Hughes 2003, Steffen 2009, IPCC 2014, Williams 2014, CSIRO 2017). Dickman (2020) and Ward *et al.* (2020) estimated that the 2019/2020 fires killed 1.3 billion animals and burned approximately 97,000 km² of habitat. Hence, Australian conservation planners must urgently assess the extinction vulnerability of fire-impacted species and protect populations in both burnt and unburnt areas (Ward 2020).

1.4. Australia as a world leader in mammal extinctions

1.4.1. A history of mammals in Australia

The aridity, erratic rainfall, extreme temperatures, and nutrient-poor soils of the Australian arid zone (arid and semi-arid deserts) shape its variable and flammable landscapes (Masters 1993, Allan and Southgate 2002, Holmgren *et al.* 2003). Despite hostile and unpredictable environmental conditions, the Australian arid zone supports a diverse array of life, and mammals are particularly successful. Today, central Australian deserts have predominantly hot and arid climates; however, these ecosystems have evolved over geological time (Williams 2014). Approximately 100

million years ago (myr), the Australian land surface was warm, wet and dominated by rainforest, and the continent was largely submerged beneath a shallow ocean at the time of its separation from Gondwana (McLoughlin 2001, Williams 2014). From about 45 myr, Australia continued to move north at a rate of 6/7 cm per year into the dry subtropical latitude and separated from Antarctica, with the first major indications of aridity dating back to the mid-Miocene, approximately 15 myr (Williams 2014).

Rainforest abated to dry sclerophyll woodland and a eucalypt flora adapted to frequent natural fires expanded across the continent (Williams 2014).

Throughout its evolutionary history, Australian mammals were remarkably distinctive having evolved within an isolated continent with a unique biodiversity. Megafauna species weighing more than 100 kg and up to 3,000 kg evolved during the Pleistocene, between approximately 2.6 myr to 12 thousand years (ka) before present (BP) (Long *et al.* 2002). The megafauna were continentally successful browsers of vegetation that probably affected Australia's shrubby biomass and fuel load, reducing the frequency and intensity of naturally occurring wildfires (Flannery 1990). Historically, central Australia's climate gradually oscillated over thousands of years from cool and arid glacial periods to warm and wet interglacial periods, and from the mid-Miocene (approximately 11-16 myr) central Australia began another slow process of aridification (Pittock 1988). Historical climatic changes were gradual, allowing flora and fauna species to adapt, hence, the mammalian species composition remained stable during much of the past 500 ka (Prideaux *et al.* 2007).

Humans first arrived in Australia more than 60 ka BP and promptly hunted the megafauna to extinction between approximately 40-50 ka BP (Miller *et al.* 2005, Johnson 2006). This is not unusual and occurred rapidly on most human-conquered landmasses in history (Harari 2014). More recently, the naturalisation of dingos, *Canis dingo*, in Australia began between 3-5 ka BP (Johnson 2006). Dingos are implicated in the continental extinction of two of Australia's top endemic predators, the thylacine,

Thylacinus cynocephalus, and the Tasmanian devil, *Sarcophilus harrisii* (Johnson 2006). However, the last Tasmanian thylacines were hunted to extinction by humans, *S. harrisii* survives in Tasmania only and dingos are now regarded as beneficial for their suppression of invasive mesopredators (Johnson *et al.* 2007, Letnic *et al.* 2009, 2012, Smith 2015).

1.4.2. Australian mammals within the arid zone

From the mid-1800s, early European biologists documented many mammal species that now range from threatened to extinct within Australia's central arid zone environments. For example, Spencer (1896) recorded the type specimen of the sandhill dunnart, *Sminthopsis psammophila*, during the Horn Expedition (Fig. 1-1).

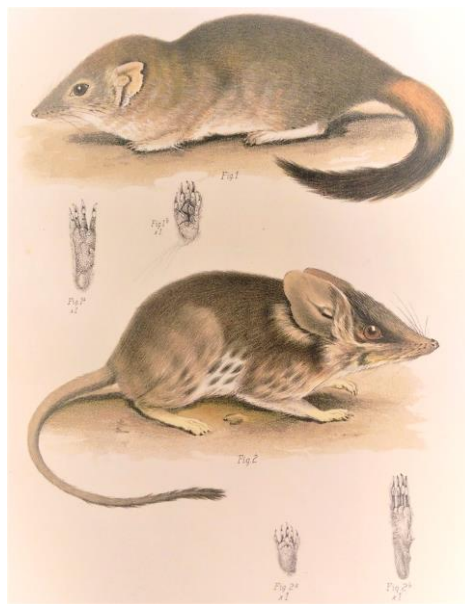


Figure 1-1. Sketches from the Horn Expedition (Spencer 1896) of a brush-tailed mulgara, *Dasycercus blythi* (top), and the type specimen of the sandhill dunnart, *Sminthopsis psammophila* (bottom).

Spencer (1896) and Finlayson (1936, 1958, 1961) observed that the common brushtail possum, *Trichosurus vulpecula*, and the greater bilby, *Macrotis lagotis*, were “ubiquitous” and “extremely common”. The rufous hare-wallaby or mala, *Lagorchestes hirsutus*, was “common” and extinct species such as the desert bandicoot, *Perameles eremiana*, and the pig-footed bandicoot, *Chaeropus ecaudatus*, were recorded in the

arid zone (Burbidge *et al.* 1988, Woinarski *et al.* 2019). The ‘Critically Endangered’ brush-tailed bettong or woylie, *Bettongia penicillata*, and threatened species that now persist only within Australia’s wetter natural refugial habitats, such as the golden bandicoot, *Isoodon auratus*, the numbat, *Myrmecobius fasciatus*, and the red-tailed phascogale, *Phascogale calura*, were also once common within the arid zone (Burbidge *et al.* 1988).

Many arid zone mammal species were protected by the First Australians who arrived on the continent at least 60 ka BP, and - prior to European contact - the arid zone mammal assemblage was diverse and stable (Roberts *et al.* 1994). However, by the early 1900s, Finlayson (1936) realised that arid zone fauna assemblage was collapsing, observing that:

“The old Australia is passing. The environment which moulded the most remarkable fauna in the world is beset on all sides by influences which are reducing it to a medley of semi-artificial environments, in which the original plan is lost and the final outcome of which no man may predict.”

A limited number of arid zone mammal species persisted until the mid-1900s but then declined sharply, first from southern areas and later from the north, which is consistent with the displacement of the First Australians and the cessation of traditional wildfire management (Finlayson 1936, 1958, 1961, Burbidge *et al.* 1988). In addition, the rapidly warming and drying climate and pastoral exploitation over the past century contributed to Australia’s prolific post-European mammal extinction crisis (Burbidge and McKenzie 1989, Woinarski *et al.* 2015, CSIRO 2017).

1.4.3. Recent mammal extinctions and conservation issues in Australia

Since its European colonisation, 34 Australian mammal species have been confirmed as extinct or extinct in the wild (Woinarski *et al.* 2019a, 2019b) (Fig. 1-2).

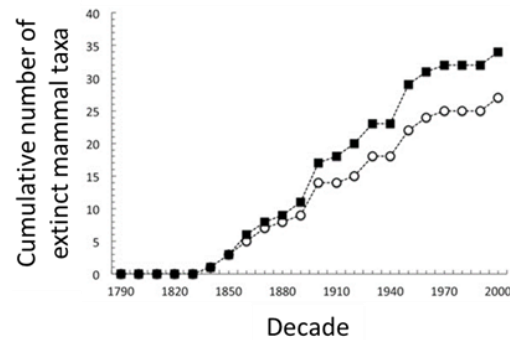


Figure 1-2. The cumulative number of extinct mammal taxa in Australia. Circles = species; squares include subspecies. NB: dates could not be estimated for some extinct taxa, so the tally given here is less than the total number of extinct taxa. The decade value refers to the decade following the date. Extracted from Woinarski *et al.* (2014).

A further 35 mammal species have contracted to less than 25 % of their original range, and without conservation, up to two threatened Australian species are predicted to become extinct in every decade in the near future (Short and Smith 1994, Burbidge *et al.* 2009, Woinarski *et al.* 2014, 2015). Many recent Australian mammal extinctions are attributed to two European-introduced invasive mesopredators, the feral cat, *Felis catus*, and the red fox, *Vulpes vulpes* (Burbidge and McKenzie 1989, Dickman 1996, Abbott 2008, Doherty 2015b). The feral cat was introduced during the mid-1800s, quickly established in less than 100 years, and is estimated to kill over one billion Australian mammals annually (Baldwin 1980, Newsome 1995, Murphy *et al.* 2019). The arid zone presented few challenges to feral cats: for example, a feral cat was reported by the Elder Expedition 400 miles from any European settlement in 1891 (Finlayson 1961, Dickman 1996). The red fox took longer to establish but did so in Victoria in 1871; it then spread continentally following the introduced rabbit, *Oryctolagus cuniculus*, and has a stable distribution throughout southern and coastal Australia (Rolls 1969, King and Smith 1985, Long 1988). Australian mammal species having a body mass between 35 g to 5.5 kg are especially threatened, as this is the prey size preferred by invasive mesopredators (Burbidge and McKenzie 1989). Australian mammal species may also be naïve of introduced European mesopredators having evolved defences, e.g. an olfactory familiarity, against native predators, such as

the quoll, *Dasyurus* spp., or members of the Thylacoleonidae family (the marsupial lions). Hence, native Australian prey species may be less cautious of unfamiliar eutherian predators (Short *et al.* 2002, Salo *et al.* 2007). European-introduced herbivores also pose a key threat in Australia, and range in size from the house mouse, *Mus musculus*, to the camel, *Camelus dromedaries* and *C. bactrianus*, causing a range of effects from outcompeting native species for primary resources to destroying natural Gnamma (water) holes whose loss is particularly detrimental for arid zone fauna (Bomford and Hart 2002, Box *et al.* 2016). Another catastrophic introduction by Europeans in the 1930s of the poisonous cane toad, *Bufo marinus*, has severely affected the tropical Australian fauna (Phillips *et al.* 2007, Shine 2010). Further extinction pressures affecting Australian mammals include habitat destruction by mining, farming and urbanisation, behavioural inabilities to adapt to environmental pressures, e.g., by requiring tree hollows as nesting sites within deforested areas, being ground-dwelling as opposed to arboreal or saxicoline (rock-dwelling), genetic isolation and inbreeding effects such as low reproductive viability, slow breeding cycles, the limited natural carrying capacity of a niche, and disease (McCallum *et al.* 1995, Smith and Quin 1996, McKenzie *et al.* 2007). Policy issues have also caused extinctions, for example, the Bramble Cay melomys, *Melomys rubicola*, the Christmas Island pipistrelle, *Pipistrellus murrayi*, and the Christmas Island forest skink, *Emoia nativitatis*, are now extinct following a lack of conservation action by the Australian Government (Martin *et al.* 2012, Woinarski *et al.* 2017).

1.4.4. Conservation management in Australia

Methods of conservation management in Australia often use invasive mesopredator control with poisons derived from several native pea species, most commonly *Gastrolobium* spp. (Wilson *et al.* 2003). Poisonous baits contain monofluoroacetic acid, the accumulation of which is lethal, but more so to introduced eutherian predators that have no evolved tolerance, whereas native carnivores are more tolerant and less

physiologically affected due to their lower metabolic rates (McIlroy 1981, Calver 1989). Conservation management includes protecting natural refugial habitats on a range of scales from entire geographic regions (National Parks or Reserves) to small, localised “microsites”, e.g., long unburned habitat patches (Reside *et al.* 2019). Natural refugial habitats in the arid zone are usually patchy and spatially unstable due to the seasonal effects of wildfires and rainfall, hence, it can be problematic to conserve these areas (Paltridge and Southgate 2001, Holmgren *et al.* 2006, Dickman *et al.* 2010, Pavey *et al.* 2014). Important conservation management methods include reintroducing dingos or ceasing dingo culling, biological controls, e.g., rabbit haemorrhagic disease (Calicivirus), floppy-top anti-predator exclosures and translocations to refuge islands or protected habitats (Morris *et al.* 2003, Wilson *et al.* 2003, Letnic *et al.* 2009). Examples of emerging management methods throughout Australian environments are strategic water and food placement (Arid Recovery Reserve 2019), deploying artificial habitats/shelters (Hellyer *et al.* 2011, Bleicher and Dickman 2020) and taste aversion training for quolls with meat pellets containing non-lethal doses of cane toad poison (O'Donnell *et al.* 2010b). There are successful large-scale conservation initiatives, such as Western Shield and the Gondwana Link project, that restore natural refugial habitats and create habitat connectivity corridors (Bradby *et al.* 2016). While environmental manipulation is occasionally used and usually beneficial in Australia, any alteration of an ecosystem should be fully researched as it can have detrimental effects (Short *et al.* 1992, Dexter *et al.* 2013).

1.4.5. Wildfire management in the Australian arid zone

Wildfire plays a dominant role in shaping ecosystems and fauna assemblages worldwide (Bowman *et al.* 2020). Hence, wildfire control is a key component of the conservation management of deserts and is an increasingly serious issue due to the human occupation of arid environments, habitat modification by invasive species and the increased frequency and prevalence of wildfires due to global warming (Scott 2000,

Brockett *et al.* 2001, Clarke *et al.* 2013, IPCC 2014, Dutta *et al.* 2016). Changes in wildfire patterns strongly affect habitat use in Earth's deserts. For example, invasive, fast-spreading and more ignitable grass species have proliferated wildfires in the Mojave Desert since the 1970s (Brooks 1999) causing changes to the success and abundance of many native species, the effective management of wildfire risk in multiple ecosystems is a key concern in the Sonoran Desert (Gray and Dickson 2015) and knowledge of a species' response to wildfire is essential for ecologically sustainable management in Australian deserts (Bradstock *et al.* 2002, Driscoll *et al.* 2010). Management of fire-prone ecosystems often uses prescribed fire to maintain biodiversity and ecosystem function (Fontaine and Kennedy 2012). However, cultural burning with traditional methods has been used for thousands of years in Australia and is particularly important for the conservation management of arid zone ecosystems to maintain an ecological balance and prevent large destructive wildfires (Burbidge *et al.* 1988, Bowman 1995, Rose 1997, Bayly 1999, Moorcroft *et al.* 2012, Pascoe 2014). Beginning in the early Palaeogene (approximately 60 myr) wildfires became a driving ecological feature in Australia, hence, most extant arid zone species are adapted to flammable habitats to some extent (Gill 1975, Roche *et al.* 1998, Crisp *et al.* 2011). Some arid zone habitats are naturally fire-resistant, e.g., salt lakes or rocky outcrops, and others are resistant due to a lack of fuel, either due to a recent natural wildfire or the purposeful removal of the fuel load by land managers (Luke and McArthur 1978). Prior to human settlement, much of the inflammable arid zone comprised large mosaics of burned and unburned habitats that were sequentially ignited by lightning (Bird *et al.* 2008). However, earlier in its history, Australia's climate was cooler, lightning strikes were less frequent, and, prior to the arrival of humans, the fuel load was probably controlled by browsing megafauna (Flannery 1990, Price and Rind 1994). Following the extinction of the megafauna, wildfires were managed within the arid zone's western deserts for 30+ ka years by the First Australians with rotational

“fire-stick farming” or small-scale patch burning (Gould 1971, Hallam 1985, Burrows *et al.* 2006). During wildfire management, the First Australians cultivated edible plants and used fire to attract food species such as some species of monitor lizard, *Varanus* spp., that prefer digging burrows in open areas to facilitate sun basking; fire was also used for signalling, tool making, cooking, heating, to clear land and for cultural ceremonies (Jones 2012). Small-scale patch burning maximised biodiversity as burned areas were small and generally recovered within twenty years, hence, habitat mosaics with differing seral stages or successional habitat states were constantly available (Gill 1975, Masters 1993, Haydon *et al.* 2000, Bird *et al.* 2008). Most arid zone habitats are now unmanaged, and summer lightning strikes are more frequent due to global warming; there is an approximate 6 % increase in global lightning frequencies for every 1 °C rise in temperature (Price and Rind 1991, 1994, Williams *et al.* 2001). Large, catastrophic wildfires are now alarmingly common in Australia and have caused the collapse of entire ecosystems (Latz and Griffin 1978, Russell-Smith *et al.* 2007). In some areas, the frequency of weekly wildfires has increased by 40 % over the past five years, and this abruptly altered pattern is most likely related to climate change (Clarke *et al.* 2013, IPCC 2014, Dutta *et al.* 2016). Wildfires either directly kill individuals (an estimated 1.3 billion animals were killed in just a few months during the 2019/2020 east coast bushfires) or have indirect effects such as habitat loss or the removal of natural primary resources (Woinarski *et al.* 2011, Dickman 2020, Ward 2020).

1.4.6. Climate change in Australia

Anthropogenic greenhouse gas emissions beginning in the industrial revolution have significantly contributed to rapid global climate change (Rosenzweig *et al.* 2008, Kerr 2011, IPCC 2014, Williams 2014). Climate change and extreme climatic events have caused species extinctions across the world. For example, in 1987, 20 species of anurans (frogs and toads) including one endemic species suddenly disappeared from the Monteverde tropical mountains in Costa Rica (Pounds *et al.* 1999) and the Bramble

Cay melomys, *Melomys rubicola*, is now extinct due to sea level rise and the disappearance of its coastal habitat (Waller *et al.* 2017, Fulton 2017). Without immediate action on climate change, up to 37 % of all global species are predicted to become extinct by 2050 (Thomas *et al.* 2004). Rapid anthropogenic climate change is perhaps the greatest existential challenge for humanity and the one of the largest threats to global biodiversity, however, for the prevention of further of climate change related extinctions, a stubborn optimistic approach to address the issue is required (Figueres and Rivett-Carnac 2020).

The pivotal factor affecting Earth's deserts is rainfall; deficits correspondingly affect primary resources, e.g., vegetation structure/density or the abundance of invertebrates, thus, reducing reproductive success in many species of small arid zone mammal, including *S. psammophila* (Fig. 1-3) (Field 1975, Neal 1982, Perrin and Swanepoel 1987, Masters 1993, Southgate and Masters 1996, Dickman *et al.* 2001, Letnic and Dickman 2010, McLean 2015).

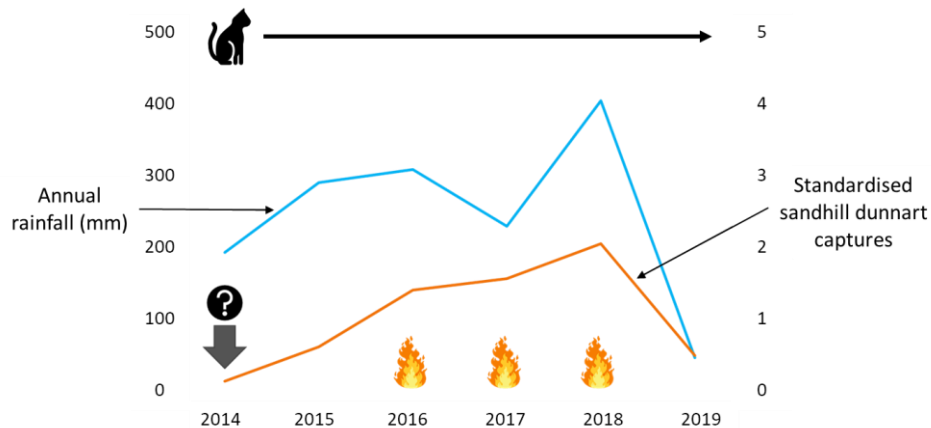


Figure 1-3. *Sminthopsis psammophila* captures (standardised per 100 trap nights; right y-axis) and annual rainfall (left y-axis) recorded at the WAGVD study site. Captures of *S. psammophila* were initially low because of habitat preference knowledge gaps (question mark symbol) but increased during the study. Captures remained stable, despite the consistent presence of the feral cat, *Felis catus* (the number of cat individuals was monitored at trapping sites with motion cameras (cat symbol). Large wildfires that occurred within the study site in 2016, 2017 and 2018 (fire symbols). However, in 2019, *S. psammophila* captures rapidly declined following a drought when annual rainfall within the study site was <50 mm.

Rainfall within arid regions is typically intermittent and related to geography, rain shadows caused by mountains, air circulation, ocean currents, climate and/or weather phenomena such as the El Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) (Williams 2014, BOM 2018). While the effects of rainfall dominate Earth's arid grassland ecosystems, there are complex relationships between fire, grazing and rainfall in creating and sustaining habitat mosaics or heterogeneous landscapes which are critical for small arid zone mammal survival (Letnic and Dickman 2006, Yarnell *et al.* 2007). Generally, high rainfall has a positive influence on small mammal abundance and diversity throughout the world (e.g., Perrin and Swanepoel 1987, Yarnell *et al.* 2007), although the lag period in population response is species specific with herbivorous species such as rodents tending to respond more quickly than carnivorous species, e.g., the Australian carnivorous marsupials (Letnic and Dickman 2005). Hence, alterations to rainfall patterns within deserts are of global concern for the conservation of small arid zone mammal species.

Climate change is predicted to continue to affect Australian arid zone mammal species more severely than elsewhere on the continent, particularly in Western Australia (Hughes 2003, Steffen 2009, CSIRO 2017). Arid zone mammal species have declined at a faster rate than elsewhere in Australia as arid zone ecosystems are sensitive, dynamic, and complex, and small variations can affect xeric biodiversity in unpredictable ways (Smith and Morton 1990, McKenzie *et al.* 2007). The first mammalian extinction successfully attributed to climate change occurred in Australia (Fulton 2017, Waller *et al.* 2017) - although there are likely other climate change related mammalian extinctions that are not published. Rapidly increasing global temperatures, increasingly irregular rainfall patterns and more frequent and extreme events such as wildfires and droughts are particularly dangerous in the Australian arid zone as water is already scarce, vegetation is highly flammable and the generally flat landscape impedes elevation shifts that allow species to compensate against rising

temperatures (Pittock 2009, Lindenmayer *et al.* 2010). The effects of climate change on species such as *S. psammophila* are not known, or incorporated into conservation planning, hence, are important knowledge gaps to address (Stewart *et al.* 2018).

1.5. The Great Victoria Desert study site

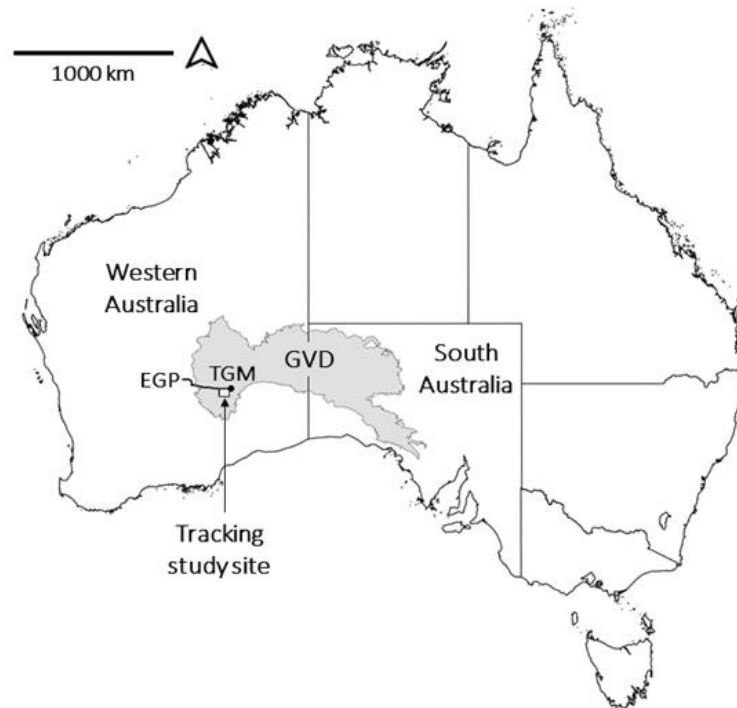


Figure 1-4. The tracking study site was within 60 km of Tropicana Gold Mine (TGM), and tracking was largely performed along the APA Eastern Goldfields Pipeline (EGP), located in the southwestern region of the Great Victoria Desert (GVD) bioregion (grey) of Western Australia. State/territory borders are indicated by black lines.

The autecological tracking study site was located in the southwest Western Australian Great Victoria Desert (WAGVD). Tracking was performed between 2015 and 2019, principally along the APA Group (APA) Eastern Goldfields Pipeline (EGP). All tracking sites were located within 60 km of Tropicana Gold Mine (TGM) at 29°14'55" S, 124°33'21" E (Fig. 1-4). The Great Victoria Desert (GVD) bioregion spans Western and South Australia and is Australia's largest desert occupying approximately 400,000 km² of the continent (IBRA 2016). The GVD is predominantly an arid sand dune desert that

receives intermittent summer and winter rainfall, has low nutrient Quaternary aeolian sandy soils over Permian and Mesozoic strata and is dominated by xeric shrubland with a low topographic relief between approximately 500-1,000 m a.s.l. (Beard 1969, Ash and Wasson 1983).

The GVD is the traditional land of several First Australian Western Desert communities, including the Tjuntjuntjara people and members of the Anangu tjuta pila nguru (Spinifex People), who sustainably managed the GVD for many tens of thousands of years (Giles 1889, Burbidge *et al.* 1988, Pascoe 2014). Until their removal by Europeans, the cultural/traditional burning land management practices of the First Australians promoted heterogeneous mosaic landscapes, which supported a flourishing fauna and flora assemblage (Gould 1971, Burbidge *et al.* 1988, Bird *et al.* 2008). The First Australians have a close and insightful knowledge of the distribution, diet, habits, reproduction and trapability of most native fauna species (Baker and Dickman 2018). Innumerable flora and fauna species feature in dreamtime knowledge passed down over thousands of years which was brutally exploited by early European expeditions to “discover” species (e.g., Clarke 2008). Their knowledge is often used to inform scientific studies as - prior to any European research - they had already determined the timing and key causes of marsupial declines across Australia, including (i) changes to indigenous land management, particularly fire regimes, (ii) overexploitation, e.g., using guns to hunt species thus quickly depleting reserves, and (iii) the pressures caused by introduced species (Baker and Dickman 2018). The First Australians have eyesight that is four times better than that of Western researchers (the best in the world), are astute fauna trackers, have advanced orientation skills and have lived sustainably in Australia for over 60 thousand years (Burbidge *et al.* 1988, Rose 1997). Thus, the First Australians are expert ecologists and conservationists and conservation management programs are doubtlessly improved with their knowledge. Globally, many studies demonstrate that ecological surveys, monitoring and large-

scale assessments benefit from reciprocal engagement with indigenous knowledge and/or multiple knowledge systems (McElwee *et al.* 2020). Further, the First Australians have tenure over large areas of land (native titles) in the arid zone, and globally, Indigenous Peoples manage or have tenure rights over at least ~38 million km² of land which is 40% of all terrestrial protected areas and ecologically intact landscapes (Garnett *et al.* 2018b).

GVD habitats contrast widely from open woodlands to chenopod and samphire shrublands, calcrete and gravel expanses, and ancient (some over four billion years old) rocky 'breakaway' cliffs, plateaus, mesas and pebbled 'gibber plains'. However, the study site in the southwest WAGVD is semi-arid due to increased winter rainfall and dominated by densely vegetated, immobile, geologically young sand dune habitats that were shaped by strong prevailing easterly winds between approximately 126-781 ka BP during the mid-Pleistocene (Madigan 1936, Sheard *et al.* 2006, Hesse 2010). Williams (2014) provides a comprehensive summary of the methods used to date desert landforms/sediments and historical climate change in deserts, e.g., thermoluminescence, cosmogenic isotopes and radiocarbon dating methods. The GVD is one of Earth's last pristine wildernesses and has not been degraded by pastoralism, hence, there are fewer impacts of dingos on human activities and dingo numbers are higher than within pastoral Australia as they are not culled frequently (Morton *et al.* 1995, Shephard 1995, Smith 2015). Although described as "lacking permanent water sources" this is somewhat misleading when applied to the GVD. There are no permanent riparian systems, however, temporary riparian systems and Gnamma holes can hold water for months following heavy rainfalls (Maclaren 1912, Bayly 2002). These water sources support water-dependent arid zone species, including humans, who transferred maps of their locations for tens of thousands of years using traditional songs, dances and art, and who managed the viability of Gnamma holes for many thousands of years (Bayly 1999). The arid interior of the GVD receives less than 125

mm of annual rainfall, whereas, in the southern and semi-arid regions of the GVD annual rainfall varies between approximately 125-525 mm due to the location of the intermittent rainfall band which moves due to ENSO effects and changes to the IOD (Ash and Wasson 1983, Nicholls 1991, BOM 2018).

The lower habitat stratum of the GVD is dominated by spinifex, *Triodia* spp., hummock grasslands that are perennial and successful in sandy antipodean habitats (Fig 1-5). Arid zone spinifex is spikey, resinous, highly flammable, and an important habitat plant as it provides protection against predators (e.g., Bos *et al.* 2002) with its sharp, neurotoxic needles. The roots of spinifex hummocks also stabilise sandy soils, such as the soils found within the southern GVD (Allan and Southgate 2002, Anderson *et al.* 2016). Shrub cover in the southern GVD is between 10-30 % of total ground cover, whereas, in northern and central regions, it is approximately 10 % or less due to the decreased volume/reliability of rainfall (Ash and Wasson 1983, Stokes 2004) (Fig. 1-5). The largest eucalypts, marble gums, *Eucalyptus gongylocarpa*, can be over 20 m high and other woodlands, e.g. mallee, *Eucalyptus* spp., *Callitris* sp. and/or *Acacia* spp. are patchily dispersed (Johnson and Burrows 1994, Shephard 1995).



Figure 1-5. Flammable, sharp, and neurotoxic spinifex, *Triodia desertorum*., hummocks (left) and the densely vegetated habitats of the southern Western Australian Great Victoria Desert (WAGVD) with *Aluta maisonneuvei* and *Callitris* sp. shrublands (right).

The southern GVD is an important natural refugial habitat and biodiversity hotspot as its dense and varied spinifex-rich habitats (Fig. 1-6 and Table 1-1) and fine yellow sandy soils have a greater water availability than the surrounding coarser red or orange sandy soils (Alizai and Hulbert 1970, Sperry and Hacke 2002).

Table 1-1. Habitat class descriptions and proportions available within the study site. Proportions were mapped within individual home ranges with satellite imagery (see Chapter 3).

Habitat class (proportion available)	Description
Swale or sand plain (0.23)	Hummock grasslands where the lower stratum is dominated by spinifex (<i>Triodia</i> spp.) up to 75 cm high with a varied middle stratum, little to no upper stratum, and sparse litter/logs. Mean gradient = 0°.
Crest (0.04)	Sand dune apexes dominated by fine yellow sandy soils and patchy, open vegetation. Where present, lower and middle stratum vegetation is intermittent spinifex or open shrubs, with a sparse upper stratum, and sparse litter and logs.
North slope (0.11)	Sloping habitat on the northern aspect of sand dunes, excluding the dune crest, with a steep gradient near crest becoming gentle then terminating where slope = 0°. Vegetation is denser than dune crest; lower stratum is dominated by spinifex of a height of up to 75 cm with a dense and varied middle stratum and sparse upper stratum, litter and logs. Usually more gradual and wider than south slope.
South slope (0.09)	Sloping habitat on the southern aspect of sand dunes, excluding the dune crest, with a steep gradient near crest becoming gentle then terminating where slope = 0°. Vegetation is denser than dune crest; lower stratum is dominated by spinifex of a height of up to 75 cm with a dense and varied middle stratum and sparse upper stratum, litter and logs. Usually steeper and not as wide as north slope.
Woodland (0.30)	Open woodland dominated by marble gums, <i>E. gongylocarpa</i> , <i>Callitris</i> sp., <i>Allocasuarina</i> spp., <i>Acacia</i> spp. (excluding <i>Acacia aneura</i> complex) and/or mallee (<i>Eucalyptus</i> spp.) dominated. Upper stratum is >2 m with a dense middle stratum and a sparse lower stratum. Dominated by dense litter and logs in ground level.
Mulga (0.21)	<i>Acacia aneura</i> complex woodland typically with clay/loam/gravel soil. Varied and dense middle stratum and a very low to no lower stratum. High proportion of litter and fallen large dead mulga trunks, logs and branches in ground level. Noticeably different soils and lacks spinifex.
Burned (0.02)	Recently burned (within the past 2 years). Absence of spinifex lower stratum, no middle or upper stratum vegetation. Bare ground and sparse burned woody debris. Sparse regenerating fire-responsive plants may be present within older burn ages.

Mulga, *Acacia aneura* complex, woodlands are typically present within clay and loam soils within the GVD and are usually resistant to smaller, cooler wildfires due to a lack of spinifex (Table 1-1 and Fig. 1-6). Complex factors dictate the locality of mulga woodlands, which are important biodiversity mediators within the GVD. However, these protective habitats can be destroyed by uncontrolled summer wildfires (Nano and Clarke 2008).

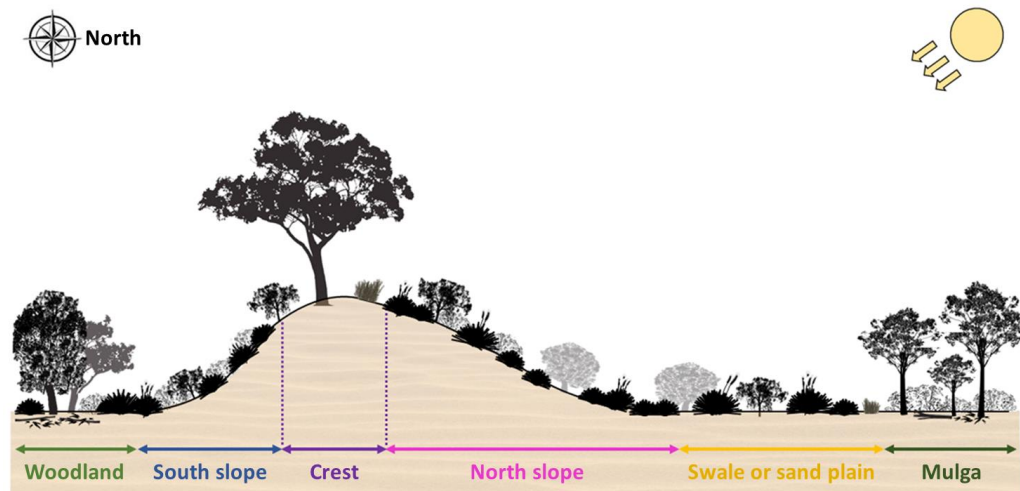


Figure 1-6. A structural cross section of habitat classes within the southern Western Australian Great Victoria Desert (WAGVD) study site. See Table 1-1 for habitat class definitions. The windward side of the dune (North slope) has a more sun exposure with a comparatively gentle/gradual slope, whereas the leeward side of the dune (South slope) habitat becomes shaded earlier and has a steeper slope.

Threatened terrestrial GVD fauna species within the WAGVD study site include the great desert skink, *Liopholis kintorei*, the southern marsupial mole, *Notoryctes typhlops*, and a mound-building megapode, the malleefowl, *Leipoa ocellata* (EPBC 1999, IUCN 2018). The remains of 11 extinct or locally extinct mammal species were recently recorded within cave deposits near the WAGVD study site, including those of the greater bilby, the golden bandicoot, the mala, the common brushtail possum, the boodie, the crescent nail-tail wallaby, *Onychogalea lunata*, the lesser stick-nest rat, *Leporillus apicalis*, the black-flanked rock wallaby, *Petrogale lateralis lateralis*, the Shark bay mouse, *Pseudomys fieldi*, the long-tailed hopping mouse, *Notomys longicaudatus*, and the red-tailed phascogale (Dr Alex Baynes and Jeff Turpin, pers.

comm.) The published key causes of GVD mammal extinctions are probably synergistic and are most often attributed to the combined effects of uncontrolled wildfires, habitat loss and surplus killings by introduced mesopredators (Burbidge and McKenzie 1989, Morris 2000, Burrows *et al.* 2006, Doherty *et al.* 2015a).

1.6. Carnivorous marsupials and the Dasyuridae

Carnivorous marsupials are endemic to Australia, the Americas, and New Guinea, however, most (99 %) species occur on one landmass only rendering them both unique and vulnerable (Baker and Dickman 2018). There are 6 families, 32 genera and 136 species of extant carnivorous marsupial worldwide (Baker and Dickman 2018). The American carnivorous marsupials often inhabit South American temperate climates and rainforests, although some species also occupy arid and semi-arid habitats, e.g., the fat-tailed mouse opossums, *Thylamys* spp., and the semi-desert dwelling Patagonian opossum, *Lestodelphys halli*, which can be found as far south as 47 °S (Baker and Dickman 2018). The most closely related true carnivorous marsupials to the Australasian group are three species of South American monito del monte, *Dromiciops* spp., however when and where they diverged remains controversial (Baker and Dickman 2018). Almost half (45 %) of all carnivorous marsupials occur only in Australia, mostly within the Dasyuromorphia, a successful and diverse order of 75 extant and extinct (e.g., the thylacine) species that originated in southern Queensland at least 55 myr (Ride 1970, Baker and Dickman 2018). There are two surviving families within the Dasyuromorphia - the Dasyuridae (dasyurids) with 58 members and the Myrmecobidae with the numbat, *M. fasciatus*, as its sole surviving member (van Dyck and Strahan 2008, Baker and Dickman 2018). There are also two endemic Australian carnivorous marsupial mole species, *Notoryctes typhlops* and *Notoryctes caurinus*, within the order Notoryctemorphia. The phylogeny of the dasyurids is well understood (Archer 1981, 1982). Genetic analyses estimated that dasyurids diversified from a

common ancestor approximately 24 myr and radiated throughout Australia and New Guinea when global temperatures decreased rapidly in the mid-Miocene, approximately 11-16 myr, and there was an Australasian land bridge (Krajewski *et al.* 2000, Archer 1981). The evolution of independent arid-adapted features are prevalent in dasyurids (e.g., evacuated palates, long tails, or granulated soles on the hind feet), indicating that convergent arid-adaptation occurred, producing superficially similar animals that are actually very diverse (Archer 1982, Morton and Baynes 1985). Most dasyurids are small “marsupial mouse” species, such as those within the *Sminthopsis* genus (Lee *et al.* 1982, Archer 1982). Thirteen species of dasyurid are classified as ‘Data Deficient’, ‘Vulnerable’, ‘Endangered’ or ‘Critically Endangered’ by the International Union for Conservation of Nature (IUCN 2020), www.iucnredlist.org). Eleven species or subspecies of dasyurid are classed as federally ‘Endangered’ by the Australian EPBC Act (1999) - the Tasmanian devil, *S. harrisii*, the northern quoll, *D. hallucatus*, the eastern quoll, *D. viverrinus*, two subspecies of the spotted-tailed quoll, *D. maculatus gracilis* and *D. maculatus maculatus*, the dibbler, *Parantechinus apicalis*, the silver-headed antechinus, *Antechinus argentus*, the black-tailed antechinus, *Antechinus arktos*, the Kangaroo Island dunnart, *S. aitkeni*, the sandhill dunnart, *S. psammophila*, and the numbat, *M. fasciatus*. The functional role of the dasyurids is widespread, for example, larger species such as the Tasmanian devil can restore top-down control in ecosystems as they remove excess resources from the environment and control invasive mesopredators, thus, increasing the abundance of small and medium sized mammals and understorey vegetation complexity (Hunter *et al.* 2015). Smaller dasyurids such as mulgara, *Dasyercus* spp., construct deep burrow systems and are ubiquitous ecosystem engineers throughout the arid zone (Ride 1970, Jones *et al.* 2003). The dasyurids are held in high regard by the First Australians for cultural practices and are prevalent in dreamtime stories, are an important food source and are sacred totem animals that are associated with traditional conservation duties towards habitat or species management (Rose 1997). Some species of dasyurid also suppress

agricultural pests, for example, in Tasmania, eastern quolls often live within farmland and consume invasive grubs, mice and insects (Jones *et al.* 2003).

A study comparing the relative abundance of skeletal remains within caves throughout Australia confirmed that arid zone dasyurid populations had declined by nearly 60 % since European colonisation, hence, the dasyurids are a key conservation target family (Morton and Baynes 1985). Reported threats to dasyurids are the rapidly expanding human population and associated habitat loss and fragmentation, predation by feral mesopredators and altered wildfire regimes (Andrew and Settle 1982, Wilson *et al.* 2003, Frank and Soderquist 2005, Dickman *et al.* 2011).

1.7. The sandhill dunnart, *Sminthopsis psammophila*: background information and knowledge gaps



Figure 1-7. The ‘Endangered’ sandhill dunnart, *Sminthopsis psammophila* (EPBC 1999).

Photo credit: Joanna Riley.

1.7.1. Known ecology

The sandhill dunnart, *Sminthopsis psammophila* (Fig. 1-7), is a federally ‘Endangered’ arid zone dasyurid that is known as the “large desert *Sminthopsis*” due to its adult body mass of between approximately 25-55 g (EPBC 1999, Menkhorst and Knight 2001).

The genus name of ‘dunnart’ was likely derived from the Nyunga (Noongar) word

“danard” (Walton and Richardson 1989). *Sminthopsis psammophila* is nocturnal and carnivorous, and most easily identified by its comparatively large mass, eyes, and pinnae, with a distinctive bicoloured fur patterning (typically grey dorsally and white ventrally with darker hair nearer the skin). The tail is particularly striking and an excellent identifier as it is clearly contrasted (dark ventrally with lighter hair dorsally) and is terminally penniform. The species also commonly has a noticeably dark-striped forehead (Fig. 1-7).

Sminthopsis psammophila was recently listed within the top five Australian mammals that are most at risk of predation by the feral cat as it (i) persists only within sensitive and unstable arid zone habitats, (ii) does not use rocky refuges, and (iii) has a body mass within the critical weight range targeted by invasive mesopredators (Woolley *et al.* 2019). *Sminthopsis psammophila* is frequently referred to as being poorly understood, enigmatic and mysterious as prior to 2015 less than 100 wild individuals had been captured (GVDBT 2017). Hence, there are few ecological studies and considerable knowledge gaps regarding the species’ physiological, morphological, and behavioural survival strategies within its hostile desert environment. Conversely, the reproductive and genetic components of the species’ conservation biology and the effect of rainfall on the population dynamics and community ecology of South Australian and captive individuals are better researched (Lambert *et al.* 2011, McLean 2015, McLean *et al.* 2018). *Sminthopsis* spp. typically survive for just one breeding year in the wild, however, males probably do not experience post-mating “male die off” as recorded in the *Antechinus*, *Parantechinus* and *Dasyurus* genera (Morton 1982, Dickman and Braithwaite 1992, Pearson and Churchill 2008). The maximum age recorded for males and females is 19 months and 25 months, respectively, but in favourable conditions both sexes have been observed breeding over two consecutive years (McLean 2015). Reproductive research on captive *S. psammophila* demonstrated it has a “Life Strategy V” (Krajewski *et al.* 2000, Lambert *et al.* 2011,

McLean 2015) - one of the six life history strategies classified by Lee *et al.* (1982) for dasyurids - as *S. psammophila* females are polyoestrous, i.e., females have multiple oestrus cycles with 22-23 days between cycles, and both sexes typically reach sexual maturity within one year and breed seasonally over an extended interval. Wild individuals usually mate following winter rains in August and September but in captivity mating is extended between June and November (Churchill 2001a and 2001b, Lambert *et al.* 2011, McLean 2015). Up to eight pouch young can be present from September in captivity although five to six are more common in the wild. Young remain in the pouch for up to 45 days and weaned young have been recorded between October and March (Lambert *et al.* 2011). Wild juveniles typically disperse between December and January and both sexes are highly mobile to track intermittent resource patches (Pearson and Robinson 1990, McLean *et al.* 2019). Droughts delay breeding and reduce the movement and survival of second year *S. psammophila* females and juveniles due to increased primary resource competition (McLean 2015); the effect of droughts on reproductive success is also demonstrated by sympatric small arid zone mammals throughout Australia (Southgate and Masters 1996, Dickman *et al.* 2001, Letnic and Dickman 2010).

The genetic structure of *S. psammophila* populations is a comparatively well-studied facet of their ecology. Comprehensive analyses of mitochondrial control region (CR) sequences and microsatellite loci by McLean *et al.* (2018) revealed that *S. psammophila* had maintained similar levels of genetic diversity to other sympatric *Sminthopsis* spp. despite its endangered status, hence, further genetic research was not identified as a significant conservation biology knowledge gap. Previously, genetic research using partial mitochondrial CR sequencing investigated 15 individuals from the EP, YRR and WAGVD populations but detected little genetic differentiation (Glen Gaikhorst, pers. comm). To re-examine this, McLean *et al.* (2014) developed 16 microsatellite markers using South Australian *S. psammophila*, establishing that the EP

and YRR populations were “recently isolated” but were likely not isolated due to the effects of European colonisation. McLean (2015) classified the behaviour of *S. psammophila* as either “resident” or “transient” with capture-recapture and mitochondrial sequencing techniques and used mitochondrial DNA (mtDNA) and microsatellite markers to produce a haplotype network, estimating that the EP and YRR populations coalesced between approximately 140-620 ka BP (McLean *et al.* 2018). There was significant differentiation between the three extant populations based on the frequency of microsatellite alleles and CR haplotypes, however, individuals within the WAGVD and YRR populations shared a mtDNA haplotype, potentially due to a lack of geographical barriers in the southern GVD (McLean *et al.* 2018). Thus, McLean *et al.* (2018) proposed that while there may be some ecological similarities between the WAGVD and YRR populations, and that the restriction of *S. psammophila* to the three known strongholds probably significantly predated the arrival of Europeans in Australia. Hence, McLean *et al.* (2018) proposed that *S. psammophila* requires conservation management as three distinct Management Units (Crandall *et al.* 2000), i.e., the WAGVD, YRR and EP populations require management separately rather than on a continental scale of Australia as per the IUCN Red List assessment (Woinarski and Burbidge 2016, IUCN 2018). Therefore, the conservation management of *S. psammophila* on a continental scale of Australia was identified as a significant area to address to improve the species’ conservation management.

As an arid zone dasyurid, the diet of *S. psammophila* was assumed to be insectivorous, generalist, opportunistic and size-dependent in order to facilitate its survival within its unpredictable desert environment (Lee *et al.* 1982, Morton *et al.* 1983, Fisher and Dickman 1992). For example, kowaris, *Dasyuroides byrnie*, (70-175 g adult body weight) consume a variety of rodents and invertebrates and even comparatively smaller dasyurids such as ningauis, *Ningauia* spp., (3.5-14 g adult body weight) and planigales, *Planigale* spp., (2.5-17 g adult body weight) attack prey that is

much larger than them (Baker and Dickman 2018). However, smaller prey may be preferred as indicated by the only dietary study for *S. psammophila* (Churchill 2001a). Thus, the species' dietary preferences were identified as an important knowledge gap to assess.

1.7.2. Conservation status

Sminthopsis psammophila is listed as 'Endangered' and protected under the Australian Federal EPBC Act (1999) having contracted to three precarious and isolated populations within Australia's southern deserts (Fig 1-7). Western Australian populations are listed as 'Endangered' by the Biodiversity Conservation Act (2016) and South Australian populations are listed as 'Vulnerable' by the National Parks and Wildlife Act (1972). After studying South Australian individuals, Churchill (2001a) recommended relisting *S. psammophila* to 'Vulnerable' as (i) five new populations were located within Eyre Peninsula (EP), the WAGVD and the Yellabinna Regional Reserve (YRR), South Australia, extending its known extent by approximately 100 km, (ii) EP *S. psammophila* appeared to be specialists, preferring specific fire history spinifex hummocks as diurnal shelters, (iii) ecological theory on South Australian *S. psammophila* could aid formal assessments and conservation management, (iv) the habitat of *S. psammophila* appeared to be extensive, and (v) potential threats were examined, but not identified. *Sminthopsis psammophila*'s IUCN Red List conservation status has been repeatedly revised between 'Data Deficient', 'Vulnerable' and 'Endangered' (IUCN 2018). In 2008 and at the beginning of this research, *S. psammophila* was listed as 'Endangered' [B2ab (ii, iii, iv, v); C1] as the known range had declined greatly, continued to decrease and the estimated area of occupancy (AOO) was <500 km² (Robinson *et al.* 2008). *Sminthopsis psammophila* was reclassified in 2016 to 'Vulnerable' [B2ab (ii, iii, v); D2] due to (i) the large, remote area between populations, (ii) a generally low survey effort, and, (iii) a larger presumed AOO of <2,000 km² (Woinarski and Burbidge 2016). This reclassification is problematic

as AOO estimates are difficult to determine for arid zone populations that are necessarily fluid and dynamic to track intermittent resources, affected by myriad immeasurable factors (due to their rarity and remote locations) and are prone to “boom and bust”. The consensus is that *S. psammophila* is severely threatened as its distribution has contracted by over 50 % (since it was first documented by Europeans) and continues to contract, there are less than 10 populations are known, there are less than 10,000 mature individuals in the wild, known populations are frequently destroyed by wildfires and its local persistence is uncertain; therefore its AOO, habitat extent, habitat quality and the number of breeding individuals are declining (Churchill 2001a, 2001b, Woinarski and Burbidge 2016).

Making accurate population density estimates for *S. psammophila* is challenging. In a key South Australian study, the population density of *S. psammophila* was estimated at 25 individuals per km² of suitable habitat (Churchill 2001a). This figure is the only population estimate used by federal legislation (Australian Government 2011) and was a projection of a maximum of five individuals captured at one 20 ha southern Australian trapping site. More often, the capture rate of *S. psammophila* is much more variable (e.g., due to droughts and deficits in resource availability) and not usually this high, hence, this population density estimate for *S. psammophila* may be overestimated (McLean 2015, Turpin and Riley 2017). The use of mark-recapture conservation biology techniques to estimate population size can be problematic for *S. psammophila*, particularly in Western Australia, as the species is not often captured, and recaptured extremely rarely. Generally, the population density of a rare arid zone species is difficult to quantify for many reasons, including variations in (i) habitat availability and habitat fragmentation, (ii) the carrying capacity for all species present, (iii) food resource abundance and dietary preferences, (iv) intra- and interspecific breeding competition, (v) shelter abundance and quality, (vi) the frequencies and impacts of wildfires, (vii) predator densities, (viii) dingo presence or absence, (ix) “boom versus

bust” population dynamics, and (x) the effect of introduced herbivores (Churchill 2001a, 2001b, Ward *et al.* 2008). Hence, there is no robust method to estimate the population size for *S. psammophila* (Woinarski and Burbidge 2016).

In summary, the conservation status of *S. psammophila* requires review due to confusion and a lack of data regarding its ecology and distribution. The increasing threat of climate change within arid Australia (Hughes 2003, Steffen 2009, IPCC 2014, CSIRO 2017) and synergistic extinction pressures (Doherty *et al.* 2015, Woolley *et al.* 2019) are immediate concerns. Conservation management plans for *S. psammophila* (e.g., Department of the Environment 2018) typically use South Australian ecological data or captive studies only, while the WAGVD *S. psammophila* population remains mostly unstudied. There are considerable knowledge gaps regarding the species’ habitat preferences, diurnal and nocturnal behaviour and adaptations, dietary requirements, and distribution - all of which affect the success of targeted surveys and conservation strategies for this rare and threatened species.

1.7.3. Historical biogeographic distribution and detection difficulties

Improving our knowledge of the current distribution of a threatened mammal species is a high priority in assessing its conservation status (e.g., Hending *et al.* 2020). In addition, it is important to predict the future range of occurrence of a threatened species and to explore the environmental variables that determine their habitat use and/or requirements (Guisan *et al.* 2013, Razgour *et al.* 2015, Russo *et al.* 2016, Jones *et al.* 2016). For data-limited species, biogeographic modelling is often used as a conservation biology tool to improve our understanding of the species’ distribution, abundance and dynamics (Rodríguez 2007). This approach is invaluable for rare arid zone species where field surveys are often challenging. First, it is essential to collate all known location records (occurrence records) for the target species, and to verify the reliability of this information.

The type specimen of *S. psammophila* was caught “with a thrown boot” during the Horn Expedition on June 18th, 1894 near Lake Amadeus in the Northern Territory (Spencer 1896), and an additional unverified record was observed near the James Range during the same expedition (Fig. 1-1 and Fig. 1-8).

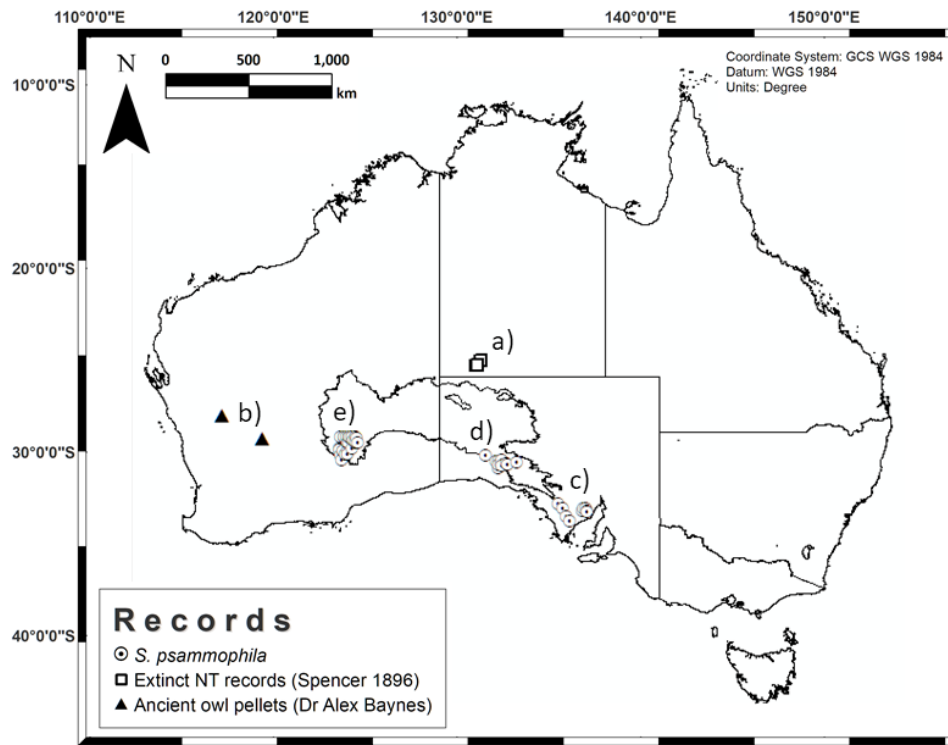


Figure 1-8. Extinct records: (a) Northern Territory (white squares) and (b) Yalgoo and Lake Barlee (black triangles; Dr Alex Baynes pers. comm.) Extant records (white circles with black dots): (c) Eyre Peninsula (EP); (d) Yellabinnia Regional Reserve (YRR); and e) Western Australian Great Victoria Desert (WAGVD). Historical occurrence records were collated at the start of this research in 2015.

Sminthopsis psammophila was subsequently confirmed from owl pellets only within Uluru’s caves in the Northern Territory and mistakenly presumed extinct (Parker 1973, Archer 1981). During 2018, Dr Alex Baynes from the Western Australian Museum verified records of ancient *S. psammophila* bones (between approximately 50 to 500 years old) that were collected near Yalgoo and Lake Barlee in Western Australia (Dr Alex Baynes, pers. comm.) (Fig.1-7). These records are discussed in Chapter 4.

Sminthopsis psammophila was not observed again until its capture in 1969 near Mamblin and Boonerdo on Eyre Peninsula (EP) in South Australia (Aitken 1971). EP is

considered the first known stronghold as the stable population has been well studied over the past decades and records from Venus Bay have been radiocarbon dated to approximately 2-3 ka BP (Baynes 1987, Copley *et al.* unpublished - from Churchill 2001a). In the 1990s, the Yellabinna Regional Reserve (YRR) in the South Australian GVD was confirmed as a second stronghold with populations located in or near Ooldea, Yarle Lakes, Mount Christie, Pinkawillinie Conservation Park and Hincks Wilderness Protected Area (Copley and Kemper 1992, Churchill 2001a, 2001b). The third stronghold is within the southwest WAGVD. Individuals were detected at Mulga Rock in 1985 and later within or near Queen Victoria Spring Nature Reserve (QVS) and throughout the southern WAGVD (Hart and Kitchener 1986, Pearson and Robinson 1990, Pearson and Churchill 2008, Turpin and Lloyd 2014, Turpin and Riley 2017). Surveying has mostly failed to record *S. psammophila* in areas between the three strongholds, however, scattered refugial populations were theorised to persist (Churchill 2001a). The naturally low population density of *S. psammophila* (between 1-6 % of all terrestrial vertebrate pitfall captures) is an important factor to consider during its ecological study and survey (McLean 2015, Turpin and Riley 2017). In addition, individuals are likely to have escaped from the standard 40 cm deep pitfall traps used in Australian fauna surveys, hence, data reporting the absence of *S. psammophila* using these trap depths are unreliable (Read *et al.* 2015). However, targeted surveys with deep (60+ cm) pitfall traps and motion cameras have also repeatedly failed to record the species, mostly in Western Australia (Burbidge *et al.* 1976, Gaikhorst and Lambert 2008, 2009 and 2014, Ecologia 2009, Ninox 2010, GHD 2010, Brennan *et al.* 2012). As extant occurrence records are limited for *S. psammophila*, and it requires remote, infrequently accessed semi-arid desert habitats, accurately determining its distribution and environmental constraints to its range were identified as key knowledge gaps in its conservation biology.

1.7.4. Habitat preferences, spinifex (*Triodia* spp.) and fire

Understanding the habitat preferences of a threatened species is essential for its conservation as natural habitats are increasingly under threat due to the effects of human overpopulation (Robinson *et al.* 2006, Butchart *et al.* 2010, Hoffmann *et al.* 2010, Dirzo *et al.* 2012). The influence that predation risk can have on habitat preferences are well established (e.g., Bowyer *et al.* 1998, Laundré *et al.* 2001, 2010, Bleicher and Dickman 2020) and the importance of productive habitats are well known for small arid zone mammals (e.g., Letnic and Dickman 2010). In Australia, the dasyurids are comparatively successful within spinifex, *Triodia* spp., hummock grasslands when contrasted with sympatric arid zone mammals in North America (Morton 1982). However, few studies investigate the specific habitat preferences of arid zone dasyurids, for example, their increased abundance within dense hummock grass understoreys (Dickman *et al.* 1993, Fisher and Dickman 1993, Bos *et al.* 2002). There is only one radio tracking study of the habitat preferences of *S. psammophila* (Churchill 2001a, 2001b). Hence, the habitat preferences of *S. psammophila* were identified as an important conservation biology knowledge gap to address.

Broadly, *S. psammophila* is reported to live on or near parallel, east-to-west oriented sand dunes with yellow, pale orange or white sandy soils (Aitken 1971, Hart and Kitchener 1986, Pearson and Churchill 2008). Spinifex (*Triodia* spp.) is usually dominant within the lower stratum of habitat, ranging from 10-90 % of total ground cover (Churchill 2001b). There are 73 described endemic *Triodia* spp. in Australia and *T. basedowii* complex hummocks are often used as a refuge in the arid zone as they are relatively common and form dense, protective, hemispherical structures (Anderson *et al.* 2016). In the preferred habitats of *S. psammophila* in the southern WAGVD, *T. basedowii* is common within darker loamy/clay soils, whereas *T. desertorum*, a comparatively slow growing and ring-forming spinifex species (Fig. 1-9), is dominant within lighter yellow/orange sandy soils often associated with sand dunes. Faster

growing *Triodia* spp. including *T. lanata*, *T. irritans* and *T. scariosa* have been recorded in habitats used by *S. psammophila* in South Australia (Aitken 1971, Pearson and Robinson 1990, Churchill 2001a, 2001b, Moseby *et al.* 2016). Common shrub species within habitats used by *S. psammophila* are *Aluta maisonneuvei*, *Thryptomene biceriata*, *Leptospermum* sp., *Hakea francisiana*, *Alyxia buxifolia*, *Eremophila scoparia*, *Senna artemissioides*, *Alectryon oleifolium* and *Grevillia* spp. while the upper stratum is dominated by marble gums, *Callitris* sp., *Acacia* spp., and mallee eucalypts (Churchill 2001a, 2001b, McLean 2015, Turpin and Riley 2017).

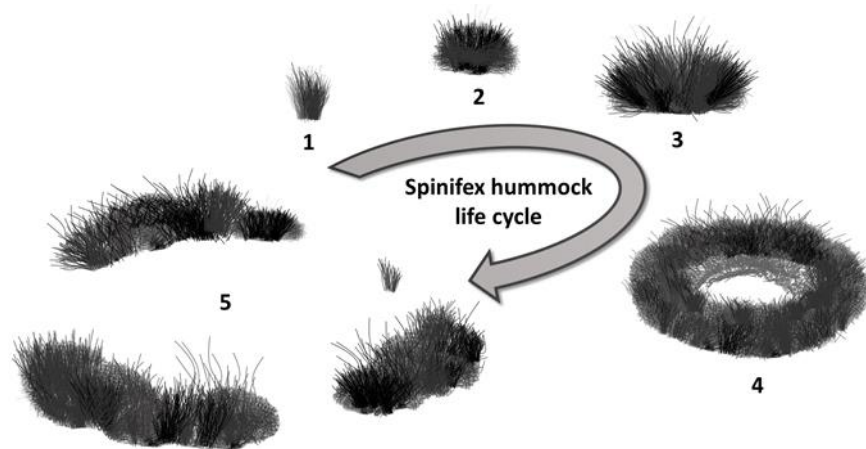


Figure 1-9. The life cycle of ring-forming spinifex hummocks, e.g., *T. desertorum*. Stage (1) new hummock, not suitable habitat; (2) small and dense, not suitable; (3) larger and accessible, suitable; (4) opens into ring, suitable; (5) breaks up, parts remain suitable. Redrawn from Churchill 2001a.

Fire age (the time since the last wildfire) is a key determinant of the habitat preferences of *S. psammophila* and many sympatric arid zone mammal species worldwide (e.g., Minnich 1983, Brooks *et al.* 1999, Gray and Dickson 2015). Knowing a species' response to fire is imperative for correct targeted survey design and site selection. Hence, it is a very important ecological variable to quantify for the effective conservation management of *S. psammophila*. However, most reported fire age habitat preferences for *S. psammophila* are extrapolated from trapping site data only with the exception of one South Australian radio tracking study (Churchill 2001a, 2001b). Radio tracking data proposed that EP *S. psammophila* preferred habitats with a fire age

between 8 and 20 years (Churchill 2001a, 2001b). More recent research in South Australia demonstrated that, while EP habitat characteristics differed between recently burned trapping sites and older sites, no significant effects of fire age class on *S. psammophila* capture rates could be detected (McLean 2015). Individuals from the WAGVD population have been captured at sites with fire ages between 8 and 40+ years (Hart and Kitchener 1986, Pearson and Robinson 1990, Turpin and Riley 2017). Fire responses by sympatric dunnart species vary, for example, the fat-tailed dunnart, *S. crassicaudata*, is fire sensitive and rouses from deep torpid states when artificially exposed to smoke (Stawski *et al.* 2015). Conversely, the hairy-footed dunnart, *S. hirtipes*, and the lesser hairy-footed dunnart, *S. youngsoni*, use recently burned, regenerating habitats to consume fire-responsive seeds (Masters 1993, Letnic and Dickman 2005). Hence, correctly quantifying the preferred fire age of the habitat of *S. psammophila*, particularly in Western Australia where studies are lacking, was identified as an important knowledge gap to address.

1.7.5. Spatial ecology and tracking of *S. psammophila*

Spatial ecology and tracking methods are cornerstones of conservation biology, and are particularly useful for the study of rare, threatened and/or cryptic species - many of which are located within arid environments (Kenward 1987, Aebischer *et al.* 1993). For example, radio tracking of the 'Vulnerable' Moorish tortoise, *Testudo graecasoussensis*, confirmed the importance of movement between feeding resources and thermal microhabitat refuges to prevent overheating in the Moroccan desert (Lagarde *et al.* 2012). Small arid zone mammal conservation has been improved by using tracking methods. For example, radio tracking of the endangered numbat, *M. fasciatus*, indicated the importance of large home ranges (up to 97 ha) in arid environments (Hayward *et al.* 2015) and the importance of termite mounds as fire refugia were confirmed by radio tracking the short-snouted elephant shrew, *Elephantulus brachyrhynchus*, in South Africa (Yarnell *et al.* 2008).

There is only one radio tracking study of South Australian *S. psammophila* (Churchill 2001a, 2001b), and there are no radio tracking studies of WAGVD individuals. Hence, the spatial ecology of *S. psammophila* was identified as an important knowledge gap to address. The EP and YRR populations are commonly reported to have a relatively small mean 100 % minimum convex polygon (MCP) home range of eight ha (Churchill 2001a, Australian Government 2011, Woinarski and Burbidge 2016). Site fidelity was demonstrated for at least eight months and home ranges were usually stable but drifted in response to rainfall. EP individuals were reported to strongly prefer ‘Stage 3’ hummocks as diurnal shelters, and this apparent specialism is often regarded as vital for *S. psammophila* throughout Australia (Hart and Kitchener 1986, Pearson and Churchill 2008, McLean 2015, Moseby 2016). Two statements from Churchill (2001a) that are commonly referenced are:

“On Eyre Peninsula, spinifex reaches the size and structure chosen by sandhill dunnarts for nest sites, five to ten years after a fire, and individual plants of suitable structure continue to be available for another ten years.”

“Over 85 percent of their nest sites occur in large spinifex hummocks of a particular structure and maturity, although this type of plant constitutes only 5 percent of the available spinifex hummocks.”

This apparent preference is an atypical behavioural response of a desert mammal to its extreme arid environment and does not agree with most predictions generated by ecological theory on small mammal survival within Earth’s deserts (see Section 1.3). Unpublished data from Churchill’s (2001b) and these statements are examined further in Chapter 2 and Chapter 3. In contrast, fluorescent-tagging of EP individuals demonstrated that burrows were preferred, whereas South Australian trapping site data analyses suggested that hummocks over 40 cm high and complex habitats with an abundance of logs are important for *S. psammophila* (Philp 2011, McLean 2015, Moseby *et al.* 2016). Hence, reported data are both limited and in conflict, and the

sheltering and habitat preferences of *S. psammophila* were identified as essential knowledge gaps to investigate.

1.7.6. The movements of sympatric arid zone mammals

The home range of a species is usually defined as the minimum area required by an individual to obtain sufficient resources such as food, shelter, and reproductive prospects, but excludes periods of vagrancy or exploration (Burt 1943). Home range estimates are important to understand the ecological requirements of a threatened species, thus, facilitating well informed conservation plans. In mammals, home range area and energetic needs typically vary according to influences such as climate and dietary strategies, i.e., carnivorous species typically require larger home range areas for food gathering compared with herbivorous species that cache food (McNab 1963). Hence, foraging is often regulated by the efficient use of food patches/resources within home ranges, i.e., optimal foraging (Cowie 1977, Brown *et al.* 1999). Home range area also affects population density which in turn influences behaviour (McNab 1963). In deserts, arid zone mammals generally have large home ranges across resource patches that maximise foraging opportunities within their unpredictable ecosystems (Brown 1988, Dickman *et al.* 1995, Schlesinger and Pilmanis 1998, Letnic 2001). Diet and foraging behaviour can affect home range size. For example, in the Kalahari Desert of South Africa, GPS tracking of the threatened Temminck's pangolin, *Smutsia temminckii*, demonstrated a mean adult home range of 6.5 km² and a wholly myrmecophagous diet, i.e., a diet comprising ants and termites only (Swart *et al.* 1999, Pieterse *et al.* 2014). Whereas, the herbivorous banner-tailed kangaroo rat, *Dipodomys spectabilis*, caches food within its centrally located burrow and has a small home range of 0.05 ha (Schroder 1979). For many of Earth's carnivorous mammal species, home range size increases with metabolic requirements, but not necessarily with body weight (Gittleman and Harvey 1982). For example, a large carnivore, the wolf, *Canis lupis*, with an average male and female adult body weight of 33 kg has a

recorded home range area of 392 km², while a much larger carnivore, the brown bear, *Ursus arctos*, has a mean adult body weight of 299 kg but a comparatively smaller home range area of 53 km² (Gittleman and Harvery 1982). When the effects of metabolic needs are removed, among ecological variables (including activity pattern, habitat, diet and zonation), only diet shows a significant influence on home range size (Gittleman and Harvey 1982).

In Australia, small arid zone mammal species such as *S. psammophila* typically have large home ranges and are mobile to track intermittent resources within their dynamic “boom versus bust” desert habitats (Dickman *et al.* 1995, Haythornthwaite and Dickman 2006, Dickman *et al.* 2010). For example, mature *S. crassicaudata* (15 g adult body mass) can travel up to five km in eight months, while two smaller (6-8 g adult body mass) dasyurids, *Planigale tenuirostris* and *P. gilesi*, travel 600-1,300 m in a just few days (Read 1987). A 12 g native rodent, the western pebble-mound mouse, *Pseudomys chapmani*, has a home range of up to 23 ha, and the largest recorded long distance movement by *S. youngsoni* is 14 km - however, the timescale for this is unknown (Dickman *et al.* 1995, Anstee *et al.* 1997). Large arid zone mammals can have vast ranges, e.g., the western quoll, *Dasyurus geoffroyi*, weighing one kg, has a home range of approximately 3,000 ha and the feral cat travels up to 230 km in its lifetime (Newsome 1995, Arid Recovery Reserve 2018). *Sminthopsis psammophila* has been recorded at speeds of one kmhr⁻¹ (Churchill 2001a, McLean 2015) and has been reported to have a maximum home range of 42 ha (Churchill 2001b). As most arid zone mammals worldwide require large home ranges to exploit the spatially and temporally variable resources of their desert environments, the small home range of eight ha for *S. psammophila* used in federal conservation advice (Australian Government 2011) is likely underestimated and detrimental for the species’ protection, i.e., smaller areas of protected habitat may not maintain a viable population. Hence,

the reported small (eight ha) home range of *S. psammophila* is identified as a key conservation biology knowledge gap.

1.8. Thesis Outline

1.8.1. Purpose of this research

In summary, *S. psammophila* is a federally 'Endangered' (EPBC 1999) arid zone marsupial with significant conservation biology knowledge gaps. The species was mistakenly presumed extinct for approximately 70 years and empirical ecological data are limited, particularly in Western Australia. There are few studies regarding the core diurnal habitat preferences (sheltering preferences) and physiological or behavioural adaptations of *S. psammophila* to its extreme desert environment. Reported data are conflicting, thus, the success of past targeted surveys may have been affected. Data are limited regarding the home range area and habitat preferences of *S. psammophila*, and the reported small (eight ha) home range of *S. psammophila* is in direct conflict with most ecological theory that small desert dwelling, arid-adapted small mammals must necessarily have large home ranges in order to exploit temporally and spatially shifting resources. Incorrectly assuming the spatial ecology of this rare and threatened species is detrimental for its conservation, the detection of *S. psammophila* has proved historically challenging and little is known of its current distribution or vulnerability to climate change. While most Australian conservation guidelines and recovery plans consider the threats of wildfire and feral mesopredators, the impacts of climate change are not typically addressed. Due to the increasingly frequent and severe climatic events in Australia, time may be critical for protecting *S. psammophila* and many threatened arid zone species globally.

1.8.2. Aims

The central aims of this research are to address the significant conservation biology knowledge gaps for *S. psammophila* identified in Section 1.7 and to improve the conservation management of the species. Central research questions are (i) How is *S. psammophila* adapted to its desert environment? (ii) How do these adaptations enable the continued presence of *S. psammophila* when numerous sympatric mammal species have become locally extinct? (iii) Do the adaptations and preferences of *S. psammophila* make it a valuable surrogate species? (iv) What are the current and future threats to *S. psammophila*? (v) What are the conservation priorities for a) *S. psammophila* and b) sympatric arid zone species? (vi) How can the methods used improve the conservation management of a) *S. psammophila* and b) sympatric arid zone species?

First, autecological and spatial methods (radio tracking, innovative GPS tracking and faecal pellet analyses) determine the species' diurnal sheltering requirements, nocturnal foraging behaviour, habitat preferences, and dietary preferences. Second, MaxEnt species distribution models (SDMs) determine the important environmental variables for the species' persistence, predict the current distribution of *S. psammophila* and detect likely sites of occurrence throughout Western Australia. Third, the effects of climate change on the past, present and future distributions of *S. psammophila* throughout Australia are investigated. Lastly, the findings of all chapters are reviewed to suggest relevant conservation management strategies for *S. psammophila* and sympatric arid zone species. Changes for Australian conservation policy and recommendations to improve the conservation management of threatened desert species globally are made.

1.8.3. Chapter summary and hypotheses

Chapter 1 introduces the concepts leading to the project's main hypotheses and aims, and information gaps are identified concerning global conservation issues, the ecology of desert species and the conservation biology of *S. psammophila*.

Chapter 2 tests the hypothesis that *S. psammophila* utilises diurnal shelters and habitats with thermal and/or anti-predation advantages that facilitate survival. The null hypothesis that diurnal shelter use by *S. psammophila* is random is tested at a range of spatial scales using radio tracking. Habitat preference characteristics at site, plot and shelter level are examined. The effects of sex, weather and reproductive status on shelter selection are determined and conservation management strategies regarding the sheltering and habitat preferences of *S. psammophila* are suggested.

Chapter 3 tests the hypothesis that certain foraging habitats with increased resources and anti-predation benefits are preferred by *S. psammophila*. The reported home range of *S. psammophila* of eight ha is investigated because arid-adapted fauna often have large home ranges and are highly mobile to track shifting resource patches.

Methods use nocturnal dusk-to-dawn radio tracking and innovative lightweight global positioning system (GPS) data loggers. Trends in habitat selection are examined using compositional foraging habitat preference analyses and the dietary preferences of *S. psammophila* and sympatric *Sminthopsis* spp. are analysed to determine whether there is dietary competition. The factors affecting diet and foraging are reviewed and conservation management recommendations are made regarding the nocturnal ecology of *S. psammophila*.

In Chapter 4, the hypothesis that natural refugial habitats are important for the conservation of threatened arid zone species is tested as *S. psammophila* appears to be restricted to favourable southern desert habitats. Presence-only MaxEnt species distribution models (SDMs) predict the current distribution of *S. psammophila* throughout Australia and ground-validation of the model's predictions in Western

Australia is performed. The results and key environmental variables for the persistence of *S. psammophila* are examined to improve the species' conservation management.

Chapter 5 investigates how SDMs can be used for conservation management. It is hypothesised that *S. psammophila* and sympatric arid zone species are highly vulnerable to anthropogenic climate change. MaxEnt SDMs and projected WorldClim GIS climate change scenarios determine the past, present and future distributions of *S. psammophila*. Conservation management recommendations under a range of future climate change scenarios for 2050 and 2070 timescales are made.

Chapter 6 considers the conclusions from the four data chapters to address the key knowledge gaps and central research questions. Conservation management solutions are provided to protect a) *S. psammophila*, b) Australian desert ecosystems and c) threatened arid zone species globally. Results are discussed regarding the aims and hypotheses of this study and are contextualised with previous published literature. Trends, ecological principles and conflicting or unexpected findings are discussed. Limitations to the research are reviewed. A brief summary of the principal implications of the findings and the significance of the study is given and recommendations are made for potential future research.

Chapter 2: Shelter types and habitat preferences



Abstract

Arid fauna species have evolved specialised adaptations due to the extreme conditions of their desert environments. Some small arid zone mammals can conserve energy and water by using thermally advantageous shelters which insulate against extreme conditions, reduce predation risk, and facilitate torpor. Understanding the sheltering and habitat preferences of a threatened species is crucial to improve its conservation biology. To quantify the diurnal sheltering requirements of a data-limited endangered desert marsupial, the sandhill dunnart, *Sminthopsis psammophila*, 40 individuals were radio tracked in the Western Australian Great Victoria Desert between 2015 and 2019. The effect of habitat class (broad habitat features), plot level (the area surrounding each shelter) and shelter characteristics (e.g., daily temperature ranges) on shelter selection and sheltering habitat preferences were assessed. Two-hundred and eleven diurnal shelters (mean of 5 ± 3 shelters per individual) were located on 363 'shelter days' (days when shelters were located), within mature vegetation (mean seral age of 32 ± 12 years post fire). Burrows were used as shelters on 77 % of shelter days and were typically concealed under mature spinifex, *Triodia* spp., with stable temperature ranges and northern aspects facing the sun. While many burrows were reused ($n = 40$ across 175 shelter days), spinifex hummock shelters were typically used for one shelter day and were not insulative against extreme temperatures. However, shallow scrapes within *Lepidobolus deserti* hummock shelters had thermal advantages, and log shelters retained heat and were selected on cooler days. *Sminthopsis psammophila* requires long unburned habitat with mature vegetation, however, unmanaged summer wildfires in the Great Victoria Desert can be extensive and destroy large areas of land, rendering them a key threat to the species. In summary, the survey and conservation of *S. psammophila* requires attention to long unburned, dense lower stratum swale, sand plain and dune slope habitats, and the tendency of *S. psammophila* to burrow allows individuals to survive within the extreme conditions of the arid zone.

2.1. Introduction

2.1.1. Overview

Correctly quantifying a threatened species' core habitat preferences is essential for understanding the species' ecology, and for improving its conservation management and mitigating threats (Brussard 1991). Habitat preference studies are widely used in Australia to gain insight into how species use their environment and to inform conservation programs (Baker and Dickman 2018) and are invaluable for worldwide mammalian conservation management. For example, Eurasian badgers, *Meles meles*, are a conservation concern in the Mediterranean lowlands; habitat analyses demonstrated a preference for well-preserved scrublands with key sheltering resources which are now preferentially protected (Revilla *et al.* 2000). In Tanzania, the population density of the eastern tree hyrax, *Dendrohyrax validus*, was positively correlated with canopy cover (and not just pristine woodland habitat); thus, the previous method of selectively logging non-habitat/food tree species is now prohibited (Topp-Jørgensen *et al.* 2008). In Australia, spatial research on the sheltering preferences of the Rottnest Island quokka, *Setonix brachyurus*, indicated novel inclinations for *Malvaceae* spp. shrubs, hence, these shrub species are now protected against further anthropogenic degradation (Poole *et al.* 2015).

The survival of any animal is primarily dependent on energy expenditure and intake and maintaining thermodynamic equilibrium (Porter and Gates 1969). Many arid zone species conserve energy by entering torpor - a controlled reduction in body temperature and basal metabolic rate (Geiser and Ruf 1995). For example, the stripe-tailed dunnart, *S. macroura*, can reduce its body temperature from 35 °C to 11.3 °C after foraging bouts, reducing its metabolic rate to 30 % of its basal metabolic rate and reducing water loss by 50 % (Geiser 2004) while the Patagonian opossum, *Lestodelphys halli*, can lower its body temperature to 7.7 °C and remain torpid for 42 hours (Baker and Dickman 2018). In addition, predation is a major selective force on

survival, i.e., animals typically prefer habitats that reduce the risk of predation and prefer habitats with a consistent “landscape of fear” (Brown *et al.* 1999, Laundré *et al.* 2001). This is demonstrated globally by many small mammals in arid environments. For example, the central Chilean common degu, *Octodon degus*, preferentially forages within a five-metre radius of its shelters to reduce perceived predation risk (Fuentes *et al.* 1983), and giving-up density (GUD) experiments (Brown 1988) demonstrated that two arid zone *Sminthopsis* spp. prefer foraging within habitats that are closer to real or artificial shelters and also forage nearer habitats with an increased lower stratum density (Baker and Dickman 2018, Bleicher and Dickman 2020). In Australia, dasyurids respond quickly to olfactory predation cues of native species such as goannas, *Varanus* spp., by moving swiftly into bolt-holes or dense vegetation, and are usually nocturnally active, avoid bright moonlight, and are camouflaged presumably to lower predation risk (Baker and Dickman 2018). Other factors influencing small mammal survival within arid environments include body size and shape, fasting endurance and fat storage (often in tails for dasyurids), panting, fur licking to simulate “sweat”, conductance of fat or fur, shivering and non-shivering thermogenesis, absorptivity of radiation, temporal activity patterns, diet, water balance, metabolism and reproduction (McNab and Morrison 1963, Porter and Gates 1969, Downs and Perrin 1990, Kinlaw 1999, Scott 2000, Schwimmer and Haim 2009, Degen 2012, Baker and Dickman 2018).

Globally, many small mammals survive in desert environments by sheltering in burrows. For example, kangaroo rats, *Dipodomys* spp., jerboas, *Allactaga* spp., gerbils, *Gerbillurus* spp., and hopping mice, *Notomys* spp., are highly successful burrowers (McNab and Morrison 1963, Downs and Perrin 1990, Kinlaw 1999, van Dyck and Strahan 2008, Schwimmer and Haim 2009). Burrows form vital micro-refuges, particularly where alternative, thermally suitable refuges are rare, that provide protection from climatic extremes, predation and fire and are linked to physiology,

movement, and diet (Kinlaw 1999). Burrows are also used for food storage, e.g., several gerbil species (*Meriones* spp. and *Rhombomys opimus*) in Mongolian and Asian deserts (Naumov and Lobachev 1975). The burrows of small arid zone mammals can have variable properties depending on the season, e.g., the jerboa, *Jaculus jaculus*, uses burrows that are approximately 25 cm deep in the winter and 70 cm deep in the summer (Ghobrial and Hodieb 1973). Burrow depth strongly influences diurnal temperature fluctuations (Goyal and Gosh 1993), for example, burrows that are 20 cm deep fluctuate by about 3 °C only (Happold 1984). While burrows have been shown to buffer against temperature extremes (Kinlaw 1999, Degen 2012), the thermal diffusivity of sandy soils, combined with shallow burrow depths require some burrowing desert species to frequently utilise torpor and passive rewarming, e.g., sun basking, to survive (Lovegrove *et al.* 1999, Pavey and Geiser 2008, Körtner *et al.* 2008). Burrows are excellent environmental modifiers but also provide anti-predation benefits that lower the risk of predation for small arid zone mammals (Reichman and Smith 1990, Bleicher and Dickman 2020). For example, the banner-tailed kangaroo rat, *Dipodomys spectabilis*, caches food within its burrow and does not forage far from the safety of its central location (Schroder 1979).

Burrows are used by a range of Australian desert dwelling mammals, for example, the greater bilby, *Macrotis lagotis*, hopping mice, *Notomys* spp., and carnivorous marsupials (dasyurids) such as mulgara, *Dasyercus* spp., and kowari, *Dasyuroides byrnie* (van Dyck and Strahan 2008). The high diversity of dasyurids across arid Australia has been linked to several specialised ecological and physiological traits enabling survival (Dickman 2003, Körtner *et al.* 2008, Waudby and Petit 2017). For example, the ability of dasyurids to enter daily torpor is critical for the conservation of energy and water, facilitates breeding and appears to prolong life span - allowing for survival in adverse drought and fire prone ecosystems (Geiser 2004). Intrinsically linked to torpor is shelter type and use, as different shelter microclimates and

substrates impact upon torpor and appear essential for physiological regulation (Körtner *et al.* 2008, Warnecke *et al.* 2008).

Burrowing is less commonly reported for *Sminthopsis* spp. (dunnarts) and few dunnart species are reported to excavate their own burrows. Most *Sminthopsis* spp. are reported to shelter under or within logs, woody debris, or dense vegetation, e.g., *S. dolichura* (Morton 1978), or utilise soil-crevices, e.g., *S. crassicaudata*, *S. macroura* and *S. douglasi* (Waudby and Petit 2017, Woolley 2017, Baker and Dickman 2018). Burrow use has been reported for *S. youngsoni*, although the species usurps the burrows of other taxa (e.g., spiders, scorpions, or rodents) rather than constructing its own burrows (Haythornthwaite and Dickman 2006, Baker and Dickman 2018).

Sminthopsis hirtipes has been recorded using the burrows of the spinifex hopping mouse, *N. alexis*, and the central netted dragon, *Ctenophorus nuchalis* (Dickman *et al.* 1993). Bleicher and Dickman (2020) also confirmed burrow use in swales by *S. hirtipes* and *S. youngsoni*. Overall, there are 12 arid zone *Sminthopsis* spp. but the role that shelter performs in physiologically sustaining these populations is poorly known. Given the high rate of mammalian decline in Australia's arid zone, coupled with the predicted warming of Australian deserts (Hughes 2003, Steffen 2009, IPCC 2014, CSIRO 2017), understanding habitat and shelter requirements is vital to dasyurid conservation, particularly to ameliorate threatening processes such as predation and wildfire (Burbidge *et al.* 1989, Short and Smith 1994, Johnson 2006, McKenzie *et al.* 2007, Woinarski *et al.* 2015).

2.1.2. The diurnal sheltering preferences of *S. psammophila*

The federally 'Endangered' sandhill dunnart, *S. psammophila*, is a semi-arid specialist that has significantly declined in range, persisting only in three widely separated populations (EPBC 1999) (Fig. 1-8). Key threats include predation and increasingly frequent droughts and wildfires (Burbidge and McKenzie 1989, Clarke *et al.* 2013, Doherty *et al.* 2015, Dutta *et al.* 2016, Woinarski and Burbidge 2016, Murphy *et al.*

2019). There are only few a studies on *S. psammophila* in South Australia (Churchill 2001a, 2001b, McLean 2015, Moseby *et al.* 2016), and the species is historically difficult to detect, particularly in Western Australia. In South Australia, *S. psammophila* has been associated with flammable spinifex, *Triodia* spp., hummock grassland habitats that often provide spikey and neurotoxic micro-refuges which reduce perceived predation risk for sympatric small mammals (Dawson and Bennett 1978, Burbidge *et al.* 1988, Churchill 2001a, Laundré *et al.* 2001, Bos *et al.* 2002, Pearson and Churchill 2008, Bleicher and Dickman 2020). While emphasis is frequently placed on spinifex for survival, the importance of burrow shelters for *S. psammophila* is overlooked. As the thermal biology and physiology of *S. psammophila* resembles other sympatric dunnarts and dasyurids (Withers and Cooper 2009), the main hypothesis of Chapter 2 is that *S. psammophila* has similar adaptations to the extreme conditions of the arid zone, including using diurnal burrows to conserve energy/water and reduce predation risk.

The diurnal shelter preferences of *S. psammophila* have been studied only once previously with radio tracking in South Australia (Churchill 2001a, 2001b). Fifteen individuals were radio tracked at two sites (Cowell and Middleback within Moola Station; 38 km apart) on Eyre Peninsula (EP) and at one site (Ooldea) in the Yellabinna Regional Reserve (YRR) (Fig. 1-8). On EP, nine individuals were tracked to 47 shelters, and in YRR, six individuals were tracked to 26 shelters. On EP, over 85 % of nest sites (shelters) were associated with large, mature 'Stage 3' spinifex hummocks that had a fire age or seral stage (the time since the last wildfire) of between five to ten years and up to 20 years (Churchill 2001a). 'Stage 3' spinifex hummocks constituted only 5 % of the locally available hummocks, hence, this apparent specialist shelter preference is often suggested as important for *S. psammophila* (Chapter 1). However, further examination of the unpublished dataset (Churchill 2001b) reveals that only 68 % of EP shelters were spherical nests within 'Stage 3' spinifex hummocks, 9 % of

shelters were within logs and 23 % of shelters were burrows. Further, 96 % of shelters located by Churchill (2001b) from the YRR population were burrows. In addition, fluorescent tagging of EP individuals by Philp (2011) demonstrated that burrows were preferred as refuges during nocturnal foraging. Thus, shelter type was considered an important preference to investigate further. Churchill (2001a) proposed that spinifex hummock shelters are adequate thermal refuges for *S. psammophila* in some cases. As the survival of small arid zone mammals in deserts is dependent upon water and energy conservation, the thermal properties of the shelters selected by *S. psammophila* were identified as important knowledge gaps to address.

There are two recent habitat preference studies of *S. psammophila* from South Australia. McLean (2015) determined that complex habitats with an abundance of logs are most important for *S. psammophila*, while Moseby *et al.* (2016) placed emphasis on spinifex hummocks over 40 cm high. However, these studies used trapping site data and no tracking methods were used. Therefore, the habitat preferences of *S. psammophila* at broad (habitat class) and local scales (plot level), e.g., habitat strata density or spinifex height, were determined as important to investigate further. As McLean (2015) determined that sex and reproductive status affected behaviour in *S. psammophila* and this has been observed in other dunnart species, e.g., *S. dolichura* (Friend *et al.* 1997) and *S. youngsoni* (Baker and Dickman 2018), the effect of sex and reproductive status were determined as important to investigate further.

There have been no further radio tracking studies of the diurnal sheltering preferences of *S. psammophila* to date. Despite the requirement for detailed habitat studies (Churchill 2001a), this is the first radio tracking assessment of *S. psammophila* in the Western Australian Great Victoria Desert (WAGVD) (Fig. 1-8). The frequently cited theory that *S. psammophila* prefer sheltering above ground in spinifex does not agree with the commonly observed and physiologically necessary subterranean sheltering behaviour recorded for sympatric small arid zone mammals worldwide. The core

sheltering and habitat preferences of a threatened species have numerous implications for their effective conservation management and are particularly important with respect to fire management in the Australian arid zone (Churchill 2001a). Thus, the diurnal sheltering preferences of *S. psammophila* are investigated further in Chapter 2.

2.1.3. Hypotheses and aims

This study addresses key knowledge gaps in the conservation biology of *S. psammophila*. The following hypotheses are tested: (i) shelters are selected within specific habitat classes, (ii) certain shelter types and/or habitat plots and their associated features are preferred by *S. psammophila*, (iii) shelter preferences differ with sex and/or reproductive status, and, (iv) shelter selection is associated with thermal properties (temperature range) of shelter type or habitat class. It is hypothesised that the thermal properties of shelters may strongly affect their use and that shelter selection may differ across populations of *S. psammophila*. The results of Chapter 2 are then used to suggest improvements for the survey and conservation management of *S. psammophila* and sympatric arid zone species.

2.2. Methods

2.2.1. Study site

Research was largely conducted along the APA Eastern Goldfields Pipeline (EGP). Individuals were diurnally tracked at 11 sites up to 60 km west of Tropicana Gold Mine (TGM) located at 29°14'55" S, 124°33'21" E and at one site 60 km south of TGM near the western terminus of the Plumridge Lakes Access Track (PLAT) (Fig. 2-1) (Appendix A). The study site topography is classified as 'Plains and dunes (longitudinal and ring dunes) with interdune corridors and plains; occasional salt pans' at a mean \pm SD elevation of 402 \pm 22 m a.s.l. (DAFWA 2014). The study site is dominated by spinifex, predominantly *T. desertorum* and *T. basedowii*, hummock grasslands with

scattered eucalypts including marble gums, *E. gongylocarpa*, situated over wattle scrub, *Acacia* spp., and mallee, *Eucalyptus* spp. (Beard *et al.* 2014) (Appendix A). The study site soils are ‘Yellow deep sand, Soil Group 446’ except for ‘Mulga’ habitat class soils where a variable depth sandy loamy clay crust is present (Schoknecht and Pathan 2013). Weather conditions of rainfall and ambient daily temperatures (°C) were recorded by the Tropicana Gold Mine (TGM) weather station.

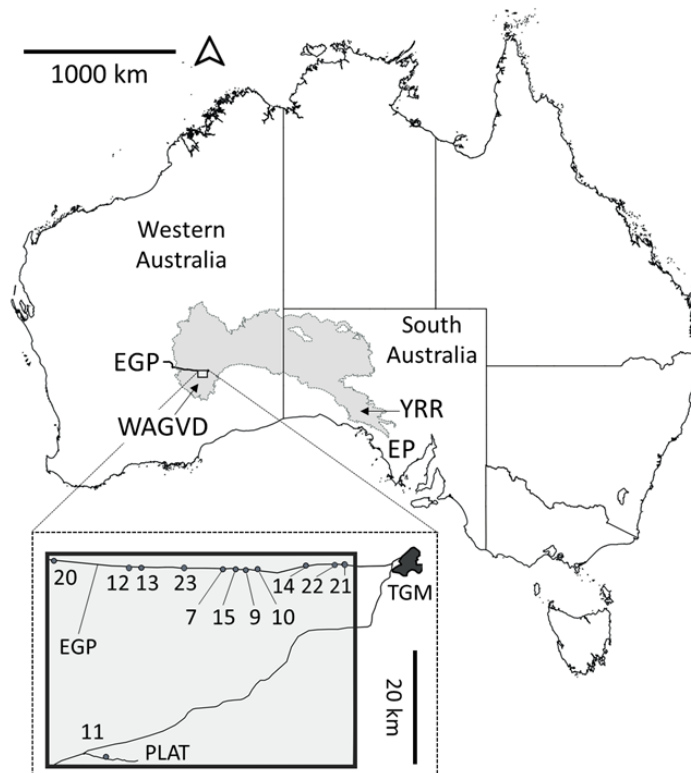


Figure 2-1. Diurnal tracking sites within the study site (inset) in the Great Victoria Desert (GVD) bioregion (grey). The three known *S. psammophila* populations are located in the Western Australian Great Victoria Desert (WAGVD), Yellabinnia Regional Reserve (YRR) and Eyre Peninsula (EP). WAGVD individuals ($n = 40$) were diurnally radio tracked at 11 sites west of Tropicana Gold Mine (TGM) near the APA Eastern Goldfields Pipeline (EGP) and Plumridge Lakes Access Track (PLAT) southwest of TGM. See Appendix A for site habitat descriptions.

2.2.2. Trapping, tagging and tracking protocol

Between 2015 and 2019, 40 individuals grouped by sex (male = M; female = F) and reproductive status (reproductively active = R; non-reproductively active = nR) as (i) RM = 15, (ii) (nRM = 10, (iii) RF = 7 or (iv) nRF = 8 were captured in pitfall traps more

than 65 cm deep [see Turpin and Riley (2017) for trapping protocol]. Trapping was performed biannually, in both the reproductively active season (September and October) and the non-reproductively active season (March and April). The reproductive status of individuals was determined by the time of year (see Chapter 1), body mass and either by pouch examination (used, with pouch young or unused) or by measuring the size of the testes. Tagging of females with large pouch young was avoided. Crown length (mm), short pes (distance in mm from posterior of heel to anterior of foot pads) and long pes (distance in mm from posterior of heel to anterior of phalanges), body mass (g), and tail length (mm) were measured, and lightweight radio transmitters ('Pip series'; 0.2-0.4 g; Biotrack Ltd., Wareham, Dorset, UK) weighing less than 5 % of an individual's body mass were attached to the lower dorsal area with cold curing tissue adhesive (Vetbond™) after clipping a small area of the fur (Kenward 1987). Individuals were radio tracked using ATS R410 scanning receivers and 3-element folding Yagi directional antennas (Advanced Telemetry Systems Australia, Queensland, Australia). Trapping, tagging and handling procedures were approved by the University of Bristol and the Department of Biodiversity, Conservation and Attractions (DBCA) ethical review committees under DBCA licence 08-001295-4. Individuals were tracked until radio transmitters naturally detached. Shelters were verified visually, and concealed burrow entrances were confirmed after radio tracking. Shelter locations were recorded using a global positioning system (GPS) device (Garmin, eTrex, 5-15 m accuracy; Garmin Europe Ltd., Romsey, UK) more than 30 minutes after sunrise to avoid disturbance. All further data, e.g., shelter characteristics, were collected after transmitters detached.

2.2.3. Shelter habitat analyses

2.2.3.1. Site level

Using satellite imagery in QGIS (QGIS Development Team 2019, Open Source Geospatial Foundation Project, www.qgis.osgeo.org), habitat maps were generated

(Chapter 3) for the home range areas of all radio tracked individuals using seven habitat classes (Table 1-1) and determined the mean \pm SD minimum fire age (the number of years since the last wildfire) of the site in each case. Minimum fire age was limited by the age of the available satellite imagery (40 years in the WAGVD). Hence, long unburned habitats were classed as 40+ years. Digitised habitat maps were ground-validated with field surveys performed during radio tracking and found to be accurate. The number of days each shelter was used (shelter days) and the number of days a shelter was used before moving to a new shelter were recorded.

2.2.3.2. Plot level

Shelter use of *S. psammophila* at the plot level was investigated by using 25 m² shelter plots ($n = 211$) surrounding each centrally located shelter. Shelter plots were compared with an equal number of paired, randomly selected 25 m² plots ($n = 211$) assigned in QGIS within individual home range areas. Plot characteristics measured in the field included floristic richness (sum of living species per plot), dominant *Triodia* spp. present (either *T. desertorum*, *T. basedowii* or *T. sp. rigidissima*), hummock life stage, from 'Stage 1' to 'Stage 5' (Fig. 1-9), terrain slope (°) that was measured using an inclinometer application (Clinometer; Stephanskirchen, Germany; www.plaincode.com), and terrain aspect (either north-facing, south-facing or flat). In addition, elevation (m a.s.l.) and the distances (m) of shelters to the nearest dune crest (dist.Crest) in QGIS examined if shelters were selected at particular elevations and to assess whether the conservation of dune crests alone is sufficient to protect *S. psammophila*. Plot variables were selected by reviewing previous habitat preference analyses on *S. psammophila* and by reviewing studies of sympatric small arid zone mammals (e.g., Morton *et al.* 1983).

To investigate whether *S. psammophila* selected shelters within plots of a particular stratum density, the proportion of ground level, lower, and middle strata within shelter and random plots were compared. Habitat strata density was measured due to the

previous conflicting habitat preference features identified as important for *S. psammophila* (Churchill 2001a, McLean 2015, Moseby *et al.* 2016). Habitat density is indicated as important for many sympatric arid zone mammals (Masters 1993, Letnic and Dickman 2010, Haslem *et al.* 2011, Baker and Dickman 2018). Structural habitat strata were classified as follows: (i) Ground = the sum of the proportions of sand, litter, logs, *Triodia* spp. and other (e.g. sedge or grass) within the plot at a height of <0.15 m; (ii) Lower = the sum of the proportions of litter, logs, *Triodia* spp. and other within the plot of height between 0.15-0.75 m; (iii) Middle = the sum of the proportion of vegetation excluding (e.g., shrubs or trees) within the plot of height between 0.75-2 m.

2.2.3.3. Shelter level

At shelter level, the dimensions and characteristics of shelters were measured but not all shelters were measured as some were occupied or inaccessible. In total, 108 burrows, 44 spinifex hummocks, 16 *Lepidobolus deserti* shelters and 6 log shelters were compared with the nearest suitable shelter of the same type at an equal number of randomly selected points assigned in QGIS within individual ranges. The number of randomly selected log shelters ($n = 18$) was tripled to improve statistical power. Only random shelters that were equal to or larger in size than the smallest shelter of its type recorded in this study were selected and shelters that were much larger than a plausible shelter for *S. psammophila* (e.g. very large log hollows) were not used. The *Schoenus hexandrus* ($n = 1$) shelter, the bark shelter ($n = 1$) and the mallee stump ($n = 1$) hollow were excluded from this analysis due to low sample sizes. Burrows were defined as subterranean excavations >8 cm deep (large enough to fully conceal an individual *S. psammophila*). Burrow dimensions recorded included entrance width, height and depth (cm), and entrance aspect (north, south, east or west). Hummock shelter species included *Triodia desertorum*, *T. basedowii*, *T. sp. rigidissima*, *L. deserti* and *Schoenus hexandrus*. *Lepidobolus deserti* shelters occasionally had shallow central excavations <5 cm deep that were not present in other hummock shelters.

Hummock shelter life stages were recorded from 'Stage 1' to 'Stage 5' (Fig. 1-9). Log shelters were hollows within *Eucalyptus* sp., *E. trivalva*, and *Callitris* sp. and the piece of bark and the hollow within the burned mallee stump were *Eucalyptus* sp.

Characteristics of the vegetation that covered each shelter, when present, were recorded, e.g., the nearest *Triodia* spp., dimensions and life stage.

2.2.3.4. Temperature

To examine the microclimatic effect of shelter type, Thermochron iButton temperature data loggers (iButtons) (Model: DS1921G, Maxim/Dallas Semiconductor, Texas, USA, www.ibutton.com) were deployed to record daily temperature ranges within shelters ($n = 6$ burrows, $n = 5$ spinifex hummocks, $n = 5$ *L. deserti* hummocks, $n = 3$ logs, $n = 1$ *S. hexandrus* hummock and $n = 1$ hollow in mallee stump) for a mean of 56 ± 33 days per shelter. iButtons were deployed after radio tracking in unoccupied shelters in the positions where individuals had sheltered; all shelter types were measured excluding the piece of bark that was occupied. Control iButtons were deployed at ground level within two metres of shelters and all iButtons were deployed within similar arboreal shade levels. Replicated tests using iButtons recorded the daily temperature ranges of all habitat classes, excluding 'Woodland' and 'Burned' habitats that were used infrequently by *S. psammophila* during this study, to determine whether the habitat classes used by *S. psammophila* had differing mean daily temperatures.

2.2.4. Statistical analyses

2.2.4.1. Site level analysis

At site level, a Chi square analysis with Yate's correction ['Crest' habitats had an expected value ($n = 8$ shelters) that was $<5\%$ of total observations ($n = 210$ shelters)] examined whether individuals favoured shelters within a particular habitat class. The observed number of shelters recorded in each habitat class was divided by the total number of shelters located in the study site to assess if it departed from the expected number of shelters if distributed proportionally to the area of the corresponding habitat

class available. To quantify this, the proportion available of each habitat class was calculated by dividing the sum area of each habitat class by the overall study site area (Table 1-1) (Chapter 3). 'Burned' habitat was excluded from the Chi square analysis due to its infrequent use (2 % of the total study site and used for one shelter day only). The Z statistic was used to calculate Bonferroni's confidence intervals (Neu *et al.* 1974, Byers *et al.* 1984) and to establish whether individuals positively or negatively selected a habitat class.

2.2.4.2. Plot level analysis

To examine whether shelter plot features differed significantly from paired random plots, univariate analyses on the variables (paired t-tests with Bonferroni corrections for normal data, Wilcoxon rank sums tests for non-parametric data and Chi square tests for categorical data) were first performed (Carr *et al.* 2018). To determine which response variables contributed most to explaining the variation amongst shelter and random plots, a series of generalised linear mixed effects models (GLMMs) using maximum likelihood estimations, a binomial distribution and logit link function using the *glmmTMB* package were used (Brooks *et al.* 2017). The sampling units were plots and plot type (shelter or random) was a fixed effect. The individual and site were included as random effects to account for pseudo-replication (Bolker *et al.* 2009). Spearman's correlation tests assessed variables prior to modelling to determine multicollinearity ($|R| > 0.6$ coefficient threshold). When correlation was found, the variable with the least explanatory power was removed to simplify the model. Data were standardised using mean and standard deviation $((x-\mu)/\sigma)$ to provide useful comparisons of effect size. Akaike's Information Criterion scores for small sample sizes (AICc) identified the most parsimonious model that explained the most amount of variance. Pseudo R^2 ($1-(\text{residual deviance}/\text{null deviance})$) were applied to explain the fit of each model and a final set of the best fitting models were chosen using delta AICc ($\Delta_i \leq 2$). The model averaging approach was used on the final best models to increase precision in the

calculation of estimates and associated *SE* (Burnham and Anderson 2002). To examine whether shelter plot variables differed significantly with sex or reproductive status, two-way ANOVA with post hoc Tukey tests were used.

2.2.4.3. Shelter level analysis

At shelter level, the characteristics of shelters were compared with those of random corresponding shelters using univariate tests (paired t-tests with Bonferroni corrections for normal data, Wilcoxon rank sum tests for non-parametric data or Chi square tests for categorical data). A one-way ANOVA with a post hoc Tukey test determined whether shelter type had a significant effect on the number of days it was used (shelter days) and the number of days a shelter was used before moving to another shelter.

2.2.4.4. Temperature data analysis

The effect of temperature (°C) on shelter selection was examined by comparing daily shelter temperature ranges with control ground temperature ranges using paired t-tests with Bonferroni corrections. A one-way ANOVA determined if there was a significant effect of maximum daily temperature (°C) on the type of shelter selected and a post hoc Tukey test determined positive or negative selection. Weather data were supplied by the weather station at TGM. A one-way ANOVA and post hoc Tukey test examined the effect of habitat class on mean \pm *SD* daily temperature. All statistical analyses were performed in R 3.5.1 and RStudio 1.1.463 (R Core Team 2018, RStudio Team 2018). In all tests, significance was set at $p < 0.05$. Normally distributed variables are given as mean \pm *SD* and non-normal data as median \pm *IQR*.

2.3. Results

2.3.1. Site level

Individuals ($n = 40$) were radio tracked to 211 diurnal shelters with a mean of 5 ± 3 shelters per individual. Shelters were reused on multiple days (mean per individual = 8

± 9 shelter days). The average fire age of the study site was 32 ± 12 years (range: 0-40+ years). Weather conditions were stable from year to year, excluding a drought (<50 ml annual rainfall) in 2019 (Fig. 1-3). In the reproductive season, the maximum ambient temperature range was 26.4–31.7 °C and the minimum ambient temperature range was 9.5–14.5 °C. In the non-reproductive season, the maximum ambient temperature range was 29.2–33.1 °C and the minimum ambient temperature range was 13.9–18.2 °C. Overall, the maximum ambient temperature recorded was 47.3 °C on January 13th, 2019 and minimum ambient temperature recorded was -2.9 °C on July 5th, 2017.

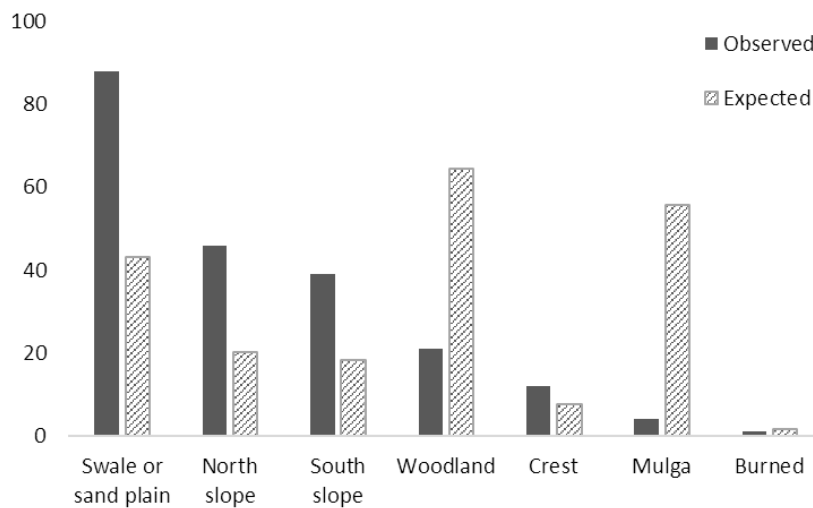


Figure 2-2. The number of shelters ($n = 211$) within each habitat class. Observed (Grey; number of shelters) and expected (striped grey; expected number of shelters if proportionally available).

Shelters were identified in all habitat classes, but shelters were not distributed as expected according to the area of each habitat class available (Chi square = 179.8, d.f. = 5, $p < 0.001$) (Fig. 2-2). 'Swale or sand plain' ($n = 88$ shelters), 'North slope' ($n = 46$ shelters) and 'South slope' ($n = 39$ shelters) habitats were positively selected, whereas 'Woodland' ($n = 12$ shelters) and 'Mulga' ($n = 4$ shelters) habitats were avoided and 'Crest' habitats were used infrequently ($n = 12$ shelters) and neither positively nor negatively selected (Table 2-1).

Table 2-1. Bonferroni's confidence intervals established positive, negative or absent habitat class selection for the shelters of *S. psammophila*. Burned habitat classes were excluded.

Habitat	Area (ha)	Number of shelters	Proportion of use expected	Proportion of use observed	Chi square value	Selection
Swale	333.5	88	0.21	0.42	44.95	Positive
North slope	155.5	46	0.10	0.22	31.60	Positive
South slope	141.1	39	0.09	0.19	22.14	Positive
Woodland	497.3	21	0.31	0.10	30.15	Negative
Crest	58.7	12	0.04	0.06	1.97	Absent
Mulga	429.2	4	0.27	0.02	49.02	Negative
Totals	1615.3	210	1.00	1.00	179.83	

2.3.2. Shelter plot characteristics

At plot level, individuals selected shelter plots with a significantly higher proportion of lower stratum habitat (0.27 ± 0.11) compared with the available proportion within random plots (0.16 ± 0.12) ($t_{210} = 9.1$, $p < 0.001$) (Fig. 2-3).

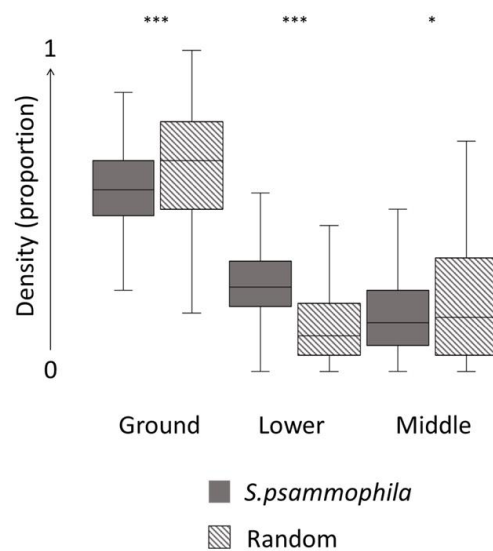


Figure 2-3. Shelter and random habitat plot densities (proportion \pm SE) of the ground level, lower stratum and middle stratum.

Shelter plots had a significantly lower proportion of ground level habitat (0.56 ± 0.12) compared with random plots (0.64 ± 0.18) ($t_{210} = -5.1$, $p < 0.001$) and a significantly

lower proportion of middle stratum habitat (0.17 ± 0.13) when compared with random plots (0.21 ± 0.18) ($t_{210} = -2.5$, $p < 0.05$). Shelter plots were significantly steeper (terrain slope = $3.9 \pm 5.3^\circ$) than random plots (terrain slope = $2.6 \pm 4.9^\circ$) ($t_{210} = 2.8$, $p < 0.001$) with a significantly lower floristic richness (4.2 ± 1.6) compared with that of random plots (4.5 ± 1.7) ($t_{210} = -2.00$, $p < 0.05$). No significant differences were detected between shelter plots and random plots with respect to dist.Crest, elevation, *Triodia* spp. or stage or terrain aspect (paired t-tests with Bonferroni corrections or Chi square tests were non-significant). *Triodia desertorum* ($n = 158$) was the dominant *Triodia* spp. within shelter plots and *T. basedowii* ($n = 24$), *T. sp. rigidissima* ($n = 23$) or no spinifex ($n = 6$) were also recorded.

Most shelters ($n = 173$) were located within 500 m of a dune crest (mean dist.Crest = 205 ± 287 m; range: 0-1125 m). However, male shelters were closer to dune crests than female shelters (Fig. 2-4).

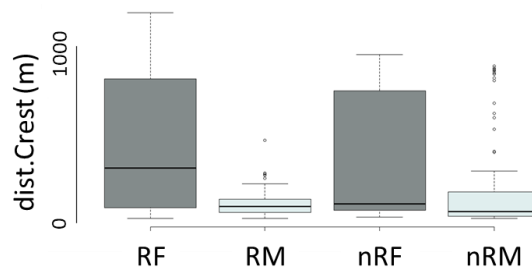


Figure 2-4. Mean \pm SE distance to dune crest (dist.Crest) in metres demonstrated significant differences in the location shelters (y-axis). R = reproductively active, nR = non-reproductively active, M = male, F = female (x-axis).

A two-way ANOVA was performed on the influence of sex and reproductive status on dist.Crest. There was a significant main effect of sex [M ($n = 133$ shelters), dist.Crest = 133 ± 213 m; F ($n = 78$ shelters), dist.Crest = 328 ± 359] ($F_{2,208} = 25.3$, $p < 0.001$). There was no significant main effect of reproductive status (R ($n = 100$ shelters), dist.Crest = 205 ± 275 ; nR ($n = 101$ shelters), dist.Crest = 205 ± 298) ($F_{2,208} = 0.04$, $p > 0.05$). The interaction effect was significant ($F_{2,208} = 8.1$, $p < 0.001$). RM shelters were significantly closer to the dune crest compared with RF shelters (Tukey test, $p < 0.001$) and nRF

shelters (Tukey test, $p < 0.01$) but not nRM shelters. nRM shelters were closer to the dune crest than RF shelters (Tukey test, $p < 0.001$) but there were no differences between the remaining groups. There was a significant effect of sex on terrain slope ($M = 4.7 \pm 6.1^\circ$; $F = 2.4 \pm 3.1^\circ$) ($W = 3803$, $p < 0.01$) but there were no other significant effects of sex or reproductive status on shelter plot variables (two-way ANOVAs were non-significant).

2.3.3. Generalised linear mixed effects models (GLMMs) for shelter and random plots

Prior to fitting models, Ground and Middle were found to be correlated ($|R| = 0.68$). As to avoid multicollinearity, Ground was removed from further models. The models that best explained differences between shelter and random plots used the variables of dist.Crest, floristic richness, Lower and terrain slope (Table 2-2).

Table 2-2. List of habitat variables from the best generalised linear mixed effects models (GLMMs) at the plot level including effect size, standard error, z statistic and p value. See Section 2.2.3. for variable units.

Model variable	Effect size	$\pm SE$	Z	P
dist.Crest	-0.19	0.12	1.5	0.13
floristic richness	-0.18	0.11	1.7	0.09
Lower	1.00	0.13	7.7	<0.001
terrain slope	0.22	0.12	1.9	0.06

The results of the GLMMs identify that lower stratum density (Lower) had a large and significant impact on shelter selection. Overall, eleven models performed well ($\Delta i \leq 2$) at explaining differences between the shelter and random plots of *S. psammophila*. A summary of the top five models are given in Table 2-3. Four of the top five models used the variable of Lower but the model that did not (terrain slope + dist.Crest) had a low Pseudo R^2 (Table 2-3), indicating again that the variable of Lower is an important determinate of the location of the diurnal shelters of *S. psammophila*.

Table 2-3. The top five most parsimonious ($\Delta i \leq 1$) and best fitting generalised linear mixed effects models (GLMMs) used to explain differences between shelter and random plots. K = the number of estimated parameters, AICc = Akaike's information criterion for small samples, Δi = the difference in AICc score compared to the most parsimonious model, ω_i = Akaike weights and Pseudo R^2 = the proportion of residual deviance explained by the model. Final models have been averaged.

Model	K	AICc	Δi	ω_i	Pseudo R^2
Lower + Middle	6	509.4	0	0.15	0.20
Lower + terrain slope	7	509.7	0.30	0.13	0.21
Lower + dist.Crest	5	510.2	0.76	0.10	0.21
terrain slope + dist.Crest	7	510.3	0.85	0.10	0.02
Lower + floristic richness	6	510.4	0.99	0.09	0.20

2.3.4. Shelter types selected by *S. psammophila*

2.3.4.1. Burrows

Sminthopsis psammophila preferred to shelter within burrows ($n = 141$) that were selected on 278 shelter days (Table 2-4). Individuals were observed excavating burrows on multiple occasions, burrows were characteristic and easily identifiable as those of *S. psammophila* (due to their dimensions and location) and fresh spoil heaps were situated at most burrow entrances. One female was recorded on video taking nesting material into a maternity burrow, while one *S. hirtipes* (that was opportunistically tracked) was recorded on video excavating its own burrow. Most burrows ($n = 130$) were concealed under mature spinifex hummocks, either under *T. desertorum* ($n = 91$), *T. basedowii* ($n = 32$) or *T. sp. rigidissima* ($n = 7$). A small number of burrows were under no vegetation ($n = 8$) or under shrubs only ($n = 3$) (Fig. 2-7). Burrow entrances were characteristic with a mean height of 4 ± 1 cm and mean width of 5 ± 0 cm. Burrow entrances were significantly smaller than random burrow entrances (height, $W = 6690$, $p < 0.05$; width, $t_{107} = 12.0$, $p < 0.05$). Burrow depths were not significantly different from the depths of random burrows (mean depth = 37 ± 42 cm; range: 5-200 cm) ($W = 4467$, $p = 0.15$). Most unoccupied measured burrow

entrances faced north ($n = 51$). Entrance aspects of south ($n = 34$), west ($n = 15$) and east ($n = 8$) were also recorded. Burrow entrance aspect was significantly different from an equal distribution (Chi square test, d.f. = 3, $p < 0.001$). RM had significantly deeper burrows (53 ± 47 cm) compared with all other groups (RF = 34 ± 28 cm; nRF = 31 ± 26 cm; nRM = 32 ± 50 cm) (Kruskal-Wallis Chi square = 11.1, d.f. = 3, $p < 0.05$ and post hoc Tukey test, $p < 0.001$ for all groups) but burrow height and width did not differ amongst groups (Kruskal-Wallis tests were not significant).

2.3.4.2. Hummock shelters (*Triodia* spp., *L. deserti* and *S. hexandrus*)

Individuals used hummock shelters ($n = 62$) that were typically used for one shelter day ($n = 64$ shelter days) (Table 2-4). Forty-five spinifex hummocks were used as shelters [*T. desertorum* ($n = 29$), *T. sp. rigidissima* ($n = 11$) and *T. basedowii* ($n = 5$)] on 46 shelter days. Sixteen *L. deserti* hummocks were used for 17 shelter days and one *S. hexandrus* hummock was used for one shelter day (Fig. 2-7). A high proportion (0.45) of spinifex hummock shelters were 'Stage 3', however, a higher proportion (0.55) were more mature ('Stage 4' to 'Stage 5'). No hummocks younger than 'Stage 3' were used as shelters. There were no significant differences between *Triodia* species and the life stage of shelter and random spinifexes (Chi square tests were not significant).

However, spinifex shelters were significantly wider ($t_{89} = 3.6$, $p < 0.05$) and taller ($t_{89} = 4.5$, $p < 0.05$) than random spinifex hummocks. The maximum width of spinifex hummock shelters was 129 ± 50 cm with a height of 45 ± 10 cm whereas random spinifex hummocks had a maximum width of 66 ± 33 cm and height of 35 ± 11 cm. *Lepidobolus deserti* shelters were classed as mature 'Stage 4' hummocks with a maximum width and height of 93 ± 16 cm and 41 ± 10 cm, respectively. Random *L. deserti* hummocks had a maximum width and height of 58 ± 39 cm and 53 ± 35 cm, respectively. *Lepidobolus deserti* shelters were significantly wider ($t_{27} = 3.2$, $p < 0.05$) but not taller than random *L. deserti* hummocks (t-tests were not significant). The *S.*

hexandrus hummock (68 cm wide by 24 cm high) was used once and was classed as mature or 'Stage 5'.

2.3.4.3. Logs and other shelters

Log shelters ($n = 6$) had a mean length of 250 ± 103 cm, width of 20 ± 5 cm and entrance diameter of 7 ± 3 cm. Log lengths and widths were not significantly different to random logs; however, entrance diameters were significantly smaller than within random logs ($t_{18} = -2.1$, $p < 0.05$). One log shelter was within a dead limb attached to a living *E. youngiana*, 0.8 m above ground, but all other log shelters were at ground level. The bark shelter (100 cm by 10 cm; entrance diameter of 4 cm) was used repeatedly ($n = 6$ shelter days) by one RF individual and a 10 cm deep hollow with a 20 cm entrance diameter within a burned mallee stump one metre above ground was used for one shelter day by a large 46 g nRM (Fig. 2-7 and Table 2-4).

2.3.5. Shelter use

Shelters ($n = 211$) were re-used on multiple days ($n = 363$ shelter days). Burrows were selected on 278 shelter days (77 % of all shelter days). All other shelter days were spinifex ($n = 46$), *L. deserti* ($n = 17$), log ($n = 14$), bark ($n = 6$), *S. hexandrus* ($n = 1$) and mallee stump ($n = 1$). Hence, there was a significant effect of shelter type on the number of shelter days used by individuals (one-way ANOVA, $F_{6, 252} = 39.7$, $p < 0.001$) (Table 2-4 and Fig. 2-5). A post hoc Tukey test showed that burrow shelter days were significantly higher than the shelter days of all other shelter types ($p < 0.001$ for all comparisons). Statistical tests showed that RM remained in the same shelter for a significantly higher number of days before moving to a new shelter compared with all other groups of nRM, RF and nRF (Kruskal-Wallis Chi square = 10.3, d.f. = 3, $p < 0.05$; pairwise Mann-Whitney test, $p < 0.001$ for all groups) and RM had significantly fewer shelters than all other groups (Kruskal-Wallis Chi square = 11.9, d.f. = 3, $p < 0.05$; pairwise Mann-Whitney test, $p < 0.001$ for all groups) (Table 2-4).

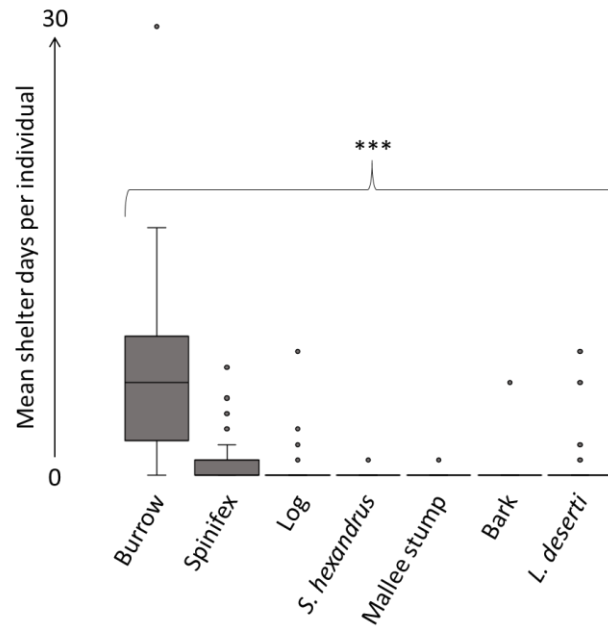


Figure 2-5. The mean \pm SE number of shelter days each shelter type was used by individuals ($n = 40$). Significant differences are indicated by *** ($p < 0.001$) and * ($p < 0.05$).

2.3.6. Temperature recordings

The daily temperature ranges of burrow shelters were significantly more stable than control ground temperature ranges ($t_5 = -7.3$, $p < 0.001$) (Table 2-5), hence, burrows were significantly insulative and provided thermodynamic benefits. The maximum ground temperature was 61 °C on November 29th, 2015 at 13:00 (ground temperatures can become very high due to reflective heat) and the minimum ground temperature was -4.5 °C on June 7th, 2017 at 05:00. In addition, *Lepidobolus deserti* shelter temperature ranges were significantly smaller than control ground temperature ranges ($t_4 = -4.0$, $p < 0.05$). No significant insulative benefits (shelter temperature ranges were not significantly different to control ground temperature ranges) were detected for spinifex or log shelters (t-tests were not significant).

However, in two log shelters, the mean diurnal temperature was 10 °C warmer than the respective control ground temperature. The maximum daily ambient temperature differed amongst shelter types (one-way ANOVA, $F_{4, 230} = 4.4$, $p < 0.01$). A post hoc Tukey test revealed that log shelters were selected on days with a significantly cooler

ambient temperature when compared with burrows, spinifex hummocks and *L. deserti* hummocks ($p < 0.01$ for all comparisons) (Fig. 2-6).

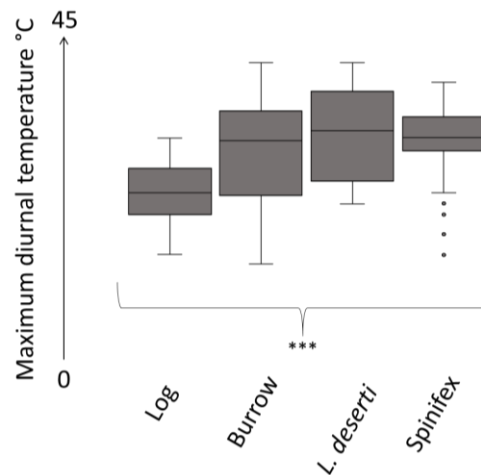


Figure 2-6. Maximum diurnal temperature \pm SE ($^{\circ}$ C) (y-axis) and the type of shelter selected (x-axis). There were significant differences in the average maximum daily temperature when log shelters were selected compared with all other measured shelters (Tukey test, $p < 0.01$, indicated by ***).

Temperature recordings of habitat classes (Table 2-6) indicated that 'North slope', 'Swale or sand plain' and 'Crest' habitats were typically warmer than other habitat classes. A one-way ANOVA indicated a significant effect of habitat class on daily mean temperature ($F_{4,1134} = 7.4$, $p < 0.001$). A post hoc Tukey test indicated that 'Swale or sand plain' and 'North slope' habitat classes had a significantly higher mean daily temperature than 'Mulga' ($p < 0.001$ for both comparisons) and 'South slope' ($p < 0.01$ for both comparisons). 'Mulga' had a significantly lower mean daily temperature compared to 'Crest' ($p < 0.05$). There were no other significant differences for the mean daily temperature within habitat classes.

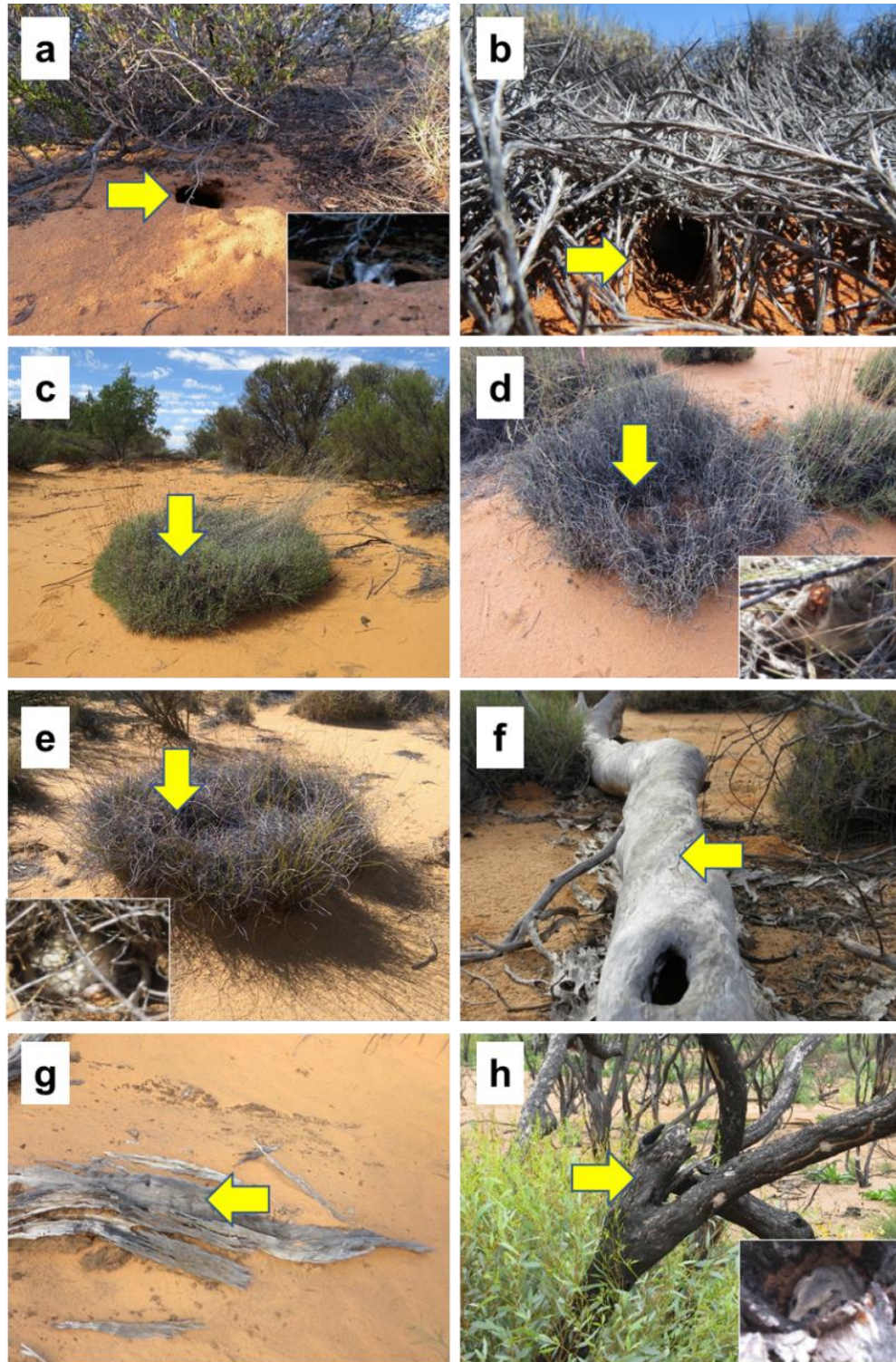


Figure 2-7. (a) Exposed burrow with emerging individual inset; (b) Concealed burrow under a 'Stage 5' *T. desertorum*; (c) 'Stage 3' *T. desertorum* hummock; (d) *L. deserti* hummock with individual inset; (e) *S. hexandrus* hummock with individual inset; (f) Log shelter; (g) Bark shelter; (h) Burned mallee stump hollow with individual inset.

Table 2-4. Shelter selection of Western Australian Great Victoria Desert (WAGVD) *S. psammophila* grouped by sex and reproductive status. Sum totals are in **bold** and mean \pm *SD* in italics.

Group (<i>n</i> individuals tracked)					Shelter days						
	Shelters	Shelter days	Days before moving	Distance between shelters (m)	Burrow	Spinifex (<i>Triodia</i> spp).	<i>L. deserti</i>	<i>S. hexandrus</i>	Log	Bark	Mallee stump
Reproductively active male (RM) (<i>n</i> = 15)	51 <i>3 \pm 2</i>	106 <i>7 \pm 5</i>	- <i>3 \pm 2</i>	- <i>212 \pm 239</i>	94 <i>6 \pm 4</i>	5 <i>0 \pm 1</i>	2 <i>0 \pm 1</i>	0 <i>0 \pm 0</i>	5 <i>0 \pm 1</i>	0 <i>0 \pm 0</i>	0 <i>0 \pm 0</i>
Non-reproductively active male (nRM) (<i>n</i> = 10)	74 <i>7 \pm 2</i>	96 <i>10 \pm 4</i>	- <i>1 \pm 0</i>	- <i>127 \pm 44</i>	62 <i>6 \pm 4</i>	18 <i>2 \pm 2</i>	14 <i>1 \pm 3</i>	0 <i>0 \pm 0</i>	1 <i>0 \pm 0</i>	0 <i>0 \pm 0</i>	1 <i>0 \pm 0</i>
Reproductively active female (RF) (<i>n</i> = 7)	36 <i>5 \pm 4</i>	83 <i>12 \pm 17</i>	- <i>1 \pm 1</i>	- <i>120 \pm 69</i>	61 <i>9 \pm 10</i>	7 <i>1 \pm 2</i>	1 <i>0 \pm 0</i>	0 <i>0 \pm 0</i>	8 <i>1 \pm 3</i>	6 <i>1 \pm 2</i>	0 <i>0 \pm 0</i>
Non-reproductively active female (nRF) (<i>n</i> = 8)	50 <i>6 \pm 4</i>	78 <i>10 \pm 4</i>	- <i>1 \pm 0</i>	- <i>100 \pm 39</i>	61 <i>8 \pm 5</i>	16 <i>2 \pm 3</i>	0 <i>0 \pm 0</i>	1 <i>0 \pm 0</i>	0 <i>0 \pm 0</i>	0 <i>0 \pm 0</i>	0 <i>0 \pm 0</i>
<i>S. psammophila</i> (<i>n</i> = 40)	211 <i>5 \pm 3</i>	363 <i>9 \pm 8</i>	- <i>2 \pm 2</i>	- <i>154 \pm 159</i>	278 <i>7 \pm 6</i>	46 <i>1 \pm 2</i>	17 <i>0 \pm 2</i>	1 <i>0 \pm 0</i>	14 <i>0 \pm 1</i>	6 <i>0 \pm 1</i>	1 <i>0 \pm 0</i>

Table 2-5. Daily temperature recordings within diurnal shelters using Thermochron iButton temperature data loggers (iButtons) compared with daily control ground temperature ranges for the diurnal shelters of Western Australian Great Victoria Desert (WAGVD) *S. psammophila*. T = temperature, min. = minimum, max. = maximum; mean \pm SD.

Shelter type	<i>n</i> iButtons (replicates)	Mean days recorded	Mean max. shelter T (°C)	Mean min. shelter T (°C)	Mean shelter T range (°C)	Mean max. control T (°C)	Mean min. control T (°C)	Mean control T range (°C)	<i>P</i> value (Paired t- test)
Burrow	6	33	31 \pm 8	15 \pm 5	16 \pm 10	46 \pm 15	5 \pm 5	40 \pm 13	$p < 0.05$
<i>Triodia</i> spp.	5	35	42 \pm 12	2 \pm 5	40 \pm 10	47 \pm 15	3 \pm 5	43 \pm 13	ns
<i>L. deserti</i>	5	26	36 \pm 7	7 \pm 6	29 \pm 7	49 \pm 12	2 \pm 6	47 \pm 9	$p < 0.05$
Log	3	39	46 \pm 7	2 \pm 5	37 \pm 3	43 \pm 17	7 \pm 5	36 \pm 14	ns
<i>S. hexandrus</i>	1	83	44	11	33	52	11	41	NA
Mallee stump	1	85	44	-0.5	45	52	-1	52	NA
Mean (all shelters ^a)	4 \pm 2	56 \pm 33	38 \pm 10	8 \pm 7	30 \pm 12	48 \pm 4	5 \pm 4	43 \pm 12	$p < 0.05$

^aBark shelter temperatures were not measured as the shelter was occupied.

Table 2-6. Daily temperature Thermochron iButton recordings within frequently used shelter habitat classes for Western Australian Great Victoria Desert (WAGVD) *S. psammophila*. T = temperature; mean \pm SD. See Table 1-1 for habitat class descriptions.

iButton replicate	Dates deployed	n days deployed	Swale or sand plain T (°C)	Crest T (°C)	North slope T (°C)	South slope T (°C)	Mulga T (°C)	Warmest habitat	Coolest habitat
1	08/03/17 - 20/03/17	20	27 \pm 11	26 \pm 10	27 \pm 11	25 \pm 8	24 \pm 9	Swale or sand plain and North slope	Mulga
2	08/03/17 - 10/04/17	33	25 \pm 12	24 \pm 10	24 \pm 11	19 \pm 8	19 \pm 10	Swale or sand plain	South slope / Mulga
3	10/04/17 - 04/07/17	85	15 \pm 7	17 \pm 10	16 \pm 13	14 \pm 9	14 \pm 12	Crest	South slope / Mulga
4	23/03/18 - 16/06/18	84	19 \pm 9	18 \pm 8	19 \pm 10	17 \pm 8	18 \pm 9	Swale or sand plain	South slope
5	10/09/18 - 29/09/19	19	28 \pm 13	28 \pm 9	30 \pm 12	27 \pm 10	26 \pm 14	North slope	Mulga
6	14/10/18 - 13/11/18	29	26 \pm 12	26 \pm 10	29 \pm 14	27 \pm 13	25 \pm 11	North slope	Mulga

2.4. Discussion

2.4.1. Overview

Shelter provides protection from climatic extremes, predation, and wildfires, and influences morphological, behavioural, and physiological adaptations in arid dwelling species worldwide (Anderson and Allred 1964, Reichman and Smith 1990, Kinlaw 1999, Scott 2000, Pavey and Geiser 2008, Körtner *et al.* 2008, Degen 2012).

Consequently, shelter requirements dictate the range and occurrence of many species, hence, an understanding of shelter is essential for biological conservation. Prior to this study (Chapter 2), the sheltering preferences of *S. psammophila* were poorly known and limited to a few analyses on outlying populations with differing results (Churchill 2001a, McLean 2015, Moseby *et al.* 2016). This detailed assessment of the shelter preferences of *S. psammophila* reveals some previously unreported characteristics and improves our understanding of the species' conservation biology, particularly in Western Australia.

2.4.2. Shelter selection of *S. psammophila*

2.4.2.1. Habitat preferences

Dune 'Crest' habitats were rarely used by *S. psammophila* during diurnal sheltering, despite the species' common name of the 'sandhill' dunnart. Instead, *S. psammophila* preferred to shelter within swales, sand plains and dune slopes with a dense lower habitat stratum and preferred vegetation of mature seral stages. 'Crest' habitats may be used infrequently due to their finer soil substrates that are inadequate for stable burrow construction (*S. psammophila* was observed excavating burrows and usually did not usurp those of other species). As temperature fluctuations are smaller in harder soils than in wind-blown, fine grain soils, this is an important arid-adaptation of *S. psammophila* shared by many small burrowing mammals in deserts (Bennett *et al.* 1988). Further, 'Crest' habitats typically lack a dense lower stratum and are popular

elevated hunting routes within the otherwise low-lying habitats of the WAGVD. As *S. psammophila* became phylogenetically distinct approximately 15 myr and GVD sand dunes were formed between only approximately 126-781 ka BP (Madigan 1936, Archer 1982), sand dunes are therefore probably not a prerequisite habitat feature for *S. psammophila*.

The dense sand plain, swale and dune slope habitats preferred by *S. psammophila* develop in the absence of wildfire (it has been over 40 years since a fire in some cases) which permits the range and abundance of sites required for adequate shelter, and lowers the risk of predation (Brown *et al.* 1999, Laundré *et al.* 2001, 2010). Hence, the conservation of long unburned spinifex grassland habitats is vital for *S.*

psammophila as it is for other sympatric taxa in the Australian arid zone (Masters 1993, Letnic and Dickman 2005, Letnic and Dickman 2010, Haslem *et al.* 2011, McLean 2015, Moseby *et al.* 2016). The importance of dense lower stratum habitats to reduce the perceived risk of predation for two sympatric arid zone *Sminthopsis* spp. has been demonstrated by Bleicher and Dickman (2020), and dense lower stratum habitats are important for many small arid zone mammals worldwide, e.g., the gray leaf-eared mouse, *G. griseoflavus*, avoids open habitats and prefers habitats with an increased density of lower stratum vegetation (Spirito *et al.* 2017). Dense habitats are particularly important in Australia as the feral cat, *Felis catus*, preferentially hunts within open habitats (McGregor *et al.* 2015, 2017). Thus, the results of Chapter 2 agree with previous ecological premise and confirm that long unburned, dense lower stratum habitats must be protected for the effective conservation of *S. psammophila*.

Interestingly, female *S. psammophila* selected sheltering habitats that were often much further away from dune crests within swales or sand plains (Fig. 2-4). This should be taken into consideration for the species' conservation management, i.e., if only habitats close to dunes are protected this may be detrimental for females and affect the reproductive success of *S. psammophila*.

2.4.2.2. Shelter types and physiology

Sminthopsis psammophila typically uses burrows as micro-refuges to maintain thermodynamic equilibrium (Porter and Gates 1969). Burrows are used by a variety of desert fauna, including *S. psammophila* (Kinlaw 1999, Scott 2000, Lovegrove *et al.* 1999, Churchill 2001a, Warnecke *et al.* 2008, Pavey and Geiser 2008, Körtner *et al.* 2008, Degen 2012). Prior to this study (Chapter 2), the importance of burrowing, torpor and passive rewarming for *S. psammophila* may have been overlooked as many *Sminthopsis* spp. are reported to inhabit other types of subterranean shelter, such as soil cracks, while few are reported to excavate their own burrows (Haythornthwaite and Dickman 2006, Waudby and Petit 2017, Baker and Dickman 2018). Several individuals were observed using sun basking (passive rewarming) at burrow entrances, particularly during cooler conditions. Passive rewarming reduces energetic costs by lowering the need for an increase in metabolic rate (Warnecke *et al.* 2008, Degen *et al.* 2012) and is facilitated by access to solar radiation, which may be improved by burrow entrance orientation (nearly 50% of the burrow entrances of *S. psammophila* faced north) and shelter selection within warmer habitat classes (Table 2-6).

The importance of burrows for *S. psammophila* may also be obscured by the popular theory that the species prefers 'Stage 3' spinifex hummocks for sheltering (Churchill 2001a). While spinifex hummocks were occasionally used as shelters, they were used infrequently and were not thermally advantageous in the WAGVD. The extreme ground temperature ranges recorded in the WAGVD (-4.5 to 61 °C) are buffered by burrowing or by the use of thermally insulative shelters (Kinlaw 1999, Degen 2012). Further, burrow use is a valuable arid zone adaptation to survive passing wildfire fronts (Friend 1993, Long 2009), which would not be possible within flammable spinifex hummocks. The spinifex hummock shelter preference theory is further rebuked by combining the dataset from Chapter 2 with Churchill's (2001b) dataset. In total, 62 % of all shelters recorded for *S. psammophila* using radio tracking have been burrows. Therefore, the

results of Chapter 2 support the premise that burrowing is an important and common adaptation for arid zone fauna (e.g., Kinlaw 1999).

However, there may be climatic or ecological differences affecting shelter selection across populations of *S. psammophila* (Churchill 2001a). Annual temperatures in WAGVD habitats are generally more extreme (BOM 2019), and WAGVD and YRR habitats are long unburned and dominated by ring-forming *T. desertorum*. Conversely, EP habitats are generally cooler (BOM 2019), more recently burned and dominated by *T. irritans* and *T. basedowii*, which are faster-growing, dome-forming species. In South Australia, dome-type spinifexes are used as shelters by *S. psammophila* (typically 'Stage 3' with a central hole that can be leaped into), and *S. ooldea* and *S. youngsoni* (smaller dunnart species) that can negotiate gaps in the dense hummocks without jumping (Churchill 2001b, Baker and Dickman 2018). Dome-forming hummocks are reported to be insulative in South Australia (Churchill 2001a), hence, may provide adequate shelter. Surface nesting is occasionally observed in small desert rodents. For example, the Karoo rat, *Otomys unisulcatus*, a South African herbivore builds nests of sticks under shrubs at about 0.45 m high that are insulative and can have a relative humidity of up to 74 % (du Plessis *et al.* 1992). However, the Karoo rat is diurnal and also alleviates extreme environmental conditions with activity patterns. As the three *S. psammophila* strongholds are estimated to have been isolated for many thousands of years, it is possible that *S. psammophila* has evolved differing sheltering behaviours across populations (McLean *et al.* 2019). Therefore, it is important that site-specific habitat characteristics, e.g., preferred *Triodia* spp. and fire age, should be taken into consideration when designing survey and conservation plans for *S. psammophila*.

Lepidobolus deserti and *S. hexandrus* are ecologically intriguing shelter choices for *S. psammophila* as their soft foliage likely provides reduced protection from predation than the ubiquitous sharp-leaved spinifex hummocks that are more commonly used by sympatric arid zone mammals (Dawson and Bennett 1978, Burbidge *et al.* 1988, Bos

et al. 2002). However, shallow scrapes within *L. deserti* shelters were thermally beneficial, indicating this may confer important fitness benefits for *S. psammophila*. Logs were important shelters for *S. psammophila* in mild conditions and are opportunistically used by other dunnart species such as *S. dolichura* and *S. crassicaudata* (Morton 1978, Friend and Pearson 1995, Churchill 2001b). Log shelters were usually warmer and selected on cooler days, potentially to aid passive rewarming (Fig. 2-6). The most unusual shelter was the mallee stump hollow used for one shelter day by a non-reproductively active male. During observation, the male moved 100 m into the nearest dense habitat but returned to the hollow prior to nocturnal foraging (Fig. 2-7). Ants were observed within the mallee stump hollow; hence, *S. psammophila* may occasionally forage diurnally during mild conditions when the benefits (e.g., access to better prey or decreased competition) of efficient foraging outweigh the costs incurred by increased exposure to predation (Fisher and Dickman 1993, Brown *et al.* 1999). Individuals may also be forced into risky decisions when resources are low (Brown *et al.* 1999). Diurnal movements between shelters were observed three further times, but were not common, and individuals moved less than 25 m. The range of shelter sites (their own burrows, the burrows of other species, logs, bark and three hummock species) selected by *S. psammophila*, which included two semi-arboreal shelters (the burned mallee stump and a high log), also indicate an opportunistic strategy by some individuals that permits a wider use of the landscape. This has been observed in a smaller dasyurid, the common planigale, *P. maculata*, which uses tree holes as well as soil cracks as shelters (Baker and Dickman 2018).

2.4.3. The sheltering adaptations of sympatric arid zone mammals

Sminthopsis psammophila shares common sheltering preferences and behavioural adaptations with many species of small desert mammal worldwide (McNab and Morrison 1963, Downs and Perrin 1990, Kinlaw 1999, Scott 2000, Schwimmer and Haim 2009, Degen 2012). These adaptations include shelter choice. For instance, the

pallid fat-tailed opossum, *Thylamys pallidior*, selects shelters within clay cracks in the Monte Desert, but also usurps the shelters of birds and lizards after consuming their eggs or young (Baker and Dickman 2018). *Sminthopsis psammophila* displays some unique sheltering characteristics amongst the Australian dasyurids. For example, While many *Sminthopsis* spp. are thought to usurp other species' burrows rather than constructing their own, thus facilitating a transient lifestyle (Haythornthwaite and Dickman 2006, Baker and Dickman 2018), *S. psammophila* often constructs its own burrows. Reproductively active males in particular invest in superior (deep) burrows and are probably territorial, as has been observed for *S. psammophila* in captivity (Lambert *et al.* 2011). This may be related to the proximity of receptive females during the reproductive season. The construction of deep burrows is energetically expensive, and their repeated use can increase predation risk. However, their constant microclimates are physiologically beneficial and are therefore worth retaining, especially for reproductively active males that have higher energetic costs due to moving long distances (up to 274 ha home range) during nocturnal activity (Chapter 3). In addition, *S. psammophila* often reuses shelter sites - particularly burrows ($n = 40$ reused over 175 shelter days) - reflecting either the paucity of suitable shelter sites across the landscape, or a benefit of burrow reuse, i.e., the physiological benefits of repeated burrow use outweigh the increased predation risk and/or an increased build-up of parasites (Baker and Dickman 2018). On average, five shelters were spaced over a mean home range of 70 ha (Chapter 3). Conversely, the threatened Julia Creek dunnart, *S. douglasi*, has much smaller home ranges [0.05-0.40 ha (Woolley 2017); 0.5-8.0 ha (Mifsud 1999)], utilises cracks or holes in clay soils and displays a reduced fidelity to shelter sites. Similarly, *S. macroura* and *S. crassicaudata* show little fidelity to their shelter sites (Waudby and Petit 2017). A high number of shelters combined with a lack of shelter fidelity led to a suggestion of serial nomadism in *S. douglasi* and *S. youngsoni* (Haythornthwaite and Dickman 2006, Woolley 2017). Substantial long-range movements and low rates of site fidelity have inferred the use of serial nomadism in *S.*

crassicaudata (Morton 1978), *Planigale gilesi* and *P. tenuirostris* (Read 1984), *S. youngsoni* and *S. dolichura* (Dickman *et al.* 1995, Haythornthwaite and Dickman 2006). Such strategies have been linked to survival in variable and resource poor arid climates. However, the apparently sedentary life strategy of some *S. psammophila* individuals infers that there are benefits to staying in one location, such as retaining information on the location of resources, e.g., mates or stable food patches (Chapter 3), rather than drifting towards opportunistic or sparse resources in unknown locations. Stable home ranges are common for many small arid zone mammals globally, for example, elephant shrews, the Macroscelididae, in the Kalahari Desert have such fidelity to their ranges that their runways are etched into the topsoil and regularly cleaned to facilitate easy movement (Baker and Dickman 2018). While some *S. psammophila* were sedentary, not all individuals reused burrows and some individuals were highly mobile (Chapter 3). Hence, *S. psammophila* may display both resident and transient sheltering behaviour as proposed by McLean *et al.* (2019).

In summary, trends in the shelter selection of *S. psammophila* are linked to the species' physiology and life in the arid zone. These results support the premise that arid zone species select shelters and sheltering habitats that have thermal advantages, enable safe and stable torpor and reduce the risk of predation (Reichman and Smith 1990, Brown *et al.* 1999, Kinlaw 1999, Laundré *et al.* 2001, 2010, Degen 2012).

2.4.4. Limitations

Data limitations of Chapter 2 include the assessment of fire age, the length of radio tracking in some cases and sex-biased results. The preferred habitat age (32+ years post fire) supporting *S. psammophila* shelters is likely underestimated as analyses were limited by the age of WAGVD satellite imagery (40 years). Improved fire age assessment methods are in progress, including *Callitris preissii* dendrochronology (O'Donnell *et al.* 2010a). Two individuals were tracked for one day only as their radio transmitters detached quickly, hence, the full scope of the sheltering behaviour of

these individuals could not be gleaned. Conversely, one female was tracked for 48 days, providing a wealth of information on the sheltering preferences of one individual. Overall, individuals were located on 9 ± 8 shelter days, hence, this study remains a comprehensive analysis of the species' sheltering preferences. Females were less readily captured and tagged than males ($F = 15$; $M = 25$), thus, stronger inferences may be placed on male sheltering preferences. However, for an endangered, rare and threatened arid zone species, 15 females is an adequate number of individuals to evaluate. Further recommendations suggest analyses of the sheltering preferences across a wider range of South Australian *S. psammophila* populations, to provide an improved comparison of the species' sheltering adaptations across Australia.

2.4.5. Conservation management

Conservation management priorities for *S. psammophila* are to protect long unburned, dense lower stratum habitats and to focus survey effort on appropriate swales, slopes, and sand plains. Conservation of dune crest habitats alone will not protect *S. psammophila*. While *S. psammophila* typically uses concealed burrows and is rare, its burrows are characteristic and are a potential identifier in the field (Fig. 2-7), although long searches may be required. In the WAGVD study site, *S. psammophila* occurs in sympatry with the brush-tailed mulgara, *D. blythi* (Baker and Dickman 2018). Burrow identifications can be made using substrate types and shelter characteristics as *D. blythi* typically shelters in deep, multi-entranced burrows supported by heavier clay soils on sand plains. Conversely, *S. psammophila* inhabits single-entranced, shallow burrows constructed on dune slopes, swales and sand plains within finer yellow to light orange soils.

Catastrophic wildfires and habitat loss are immediate concerns for *S. psammophila* (Woinarski and Burbidge 2016). The ecologically sustainable management of wildfires is central to Australian desert conservation (Bradstock *et al.* 2002, Driscoll *et al.* 2010) and the use of cultural/traditional burning is well supported for wildfire management of

the Australian arid zone (Burbidge *et al.* 1988, Bowman 1995, Rose 1997, Bayly 1999, Moorcroft *et al.* 2012, Brennan *et al.* 2012, Pascoe 2014). Hence, consultations with local indigenous experts are recommended for the correct timing, location, and scale of preventative burns. The results of Chapter 2 agree with McLean *et al.* (2019) and recommend the preservation of large contiguous areas of long unburned spinifex grassland habitat for *S. psammophila*. Predator-proof exclosures are a popular concept to conserve arid zone fauna, however, they do not appear to increase dasyurid abundance in South Australia (Moseby *et al.* 2009) and as the habitats of *S. psammophila* are highly flammable, such an approach may not be beneficial. Hence, to mitigate current threats, the preferred sheltering habitats of *S. psammophila* must be preserved, restored, and reconnected (Crooks 2006). Emerging conservation methods that may be useful include deploying artificial lower stratum structures in key habitats (Webb and Shine 2000, Bleicher and Dickman 2020) and controlling feral mesopredators in recently burned habitats (McGregor *et al.* 2015, 2017). The tendency of *S. psammophila* to occupy shallow burrows, while currently sufficient for the species' survival on the southern fringe of the arid zone, may predispose a vulnerability to anthropogenic climate change. Hence, this is an important area for further study (Chapter 5).

2.4.6. Summary

While following some general trends, the results of Chapter 2 differ to those of other tracking studies of *Sminthopsis* spp. in the arid zone. Recent advances in radio tracking technology have allowed data collection over a longer period, providing detailed insights into the species' sheltering preferences. Thus, *S. psammophila* appears unique amongst *Sminthopsis* spp. as some individuals display a high fidelity to burrows that enable survival within a hostile environment where thermally suitable shelters are rare. Burrowing often facilitates large, stable home ranges that are centred on a cluster of reused shelters, and those associated with lower stratum habitat density

(spinifex cover) provide benefits such as protection against predation during passive rewarming. However, specific shelter requirements mean *S. psammophila* is highly influenced by wildfire and is generally restricted to later seral stages of vegetation. Specific habitat requirements also influence the species' range, which is largely restricted to the southern, temperate-influenced margins of the GVD (Chapter 4). Thus, the management of *S. psammophila* must consider these preferences for its effective conservation now and in the future.

Chapter 3: Foraging, ants, and islands - the nocturnal ecology of *S. psammophila*



Abstract

Home range and foraging preference analyses are often used to improve the conservation management of threatened species. However, the ranging behaviour of threatened small desert mammals can be insufficiently understood. To address knowledge gaps in the nocturnal ecology of a poorly known desert marsupial, *Sminthopsis psammophila*, global positioning system (GPS) data loggers and radio tracking determined the ranging preferences of 24 individuals in reproductively active and non-active seasons between 2015 and 2018. Habitat preferences were analysed and the effect of sex, reproductive status and weather conditions on foraging behaviour were examined. The mean 100 % minimum convex polygon (MCP) home range area of *S. psammophila* was 70 ha. However, there was a strong effect of sex and reproductive status on ranging. Reproductively active males ($n = 9$) had a larger mean home range of 148 ha, whereas, the mean home ranges of non-reproductively active males ($n = 6$; 30 ha), non-reproductively active females ($n = 4$; 21 ha) and reproductively active females ($n = 5$; 16 ha) were comparatively smaller. Like many small desert mammals, *S. psammophila* requires dense, long unburned habitats with a high richness of shrub species and invertebrate resources during foraging. Individuals rapidly crossed tracks, open habitats and burned areas, but these areas were not commonly used during foraging bouts. The diet of *S. psammophila* contained a high proportion of ants, however, ants are not often consumed by small desert mammals due to high digestive costs. Digestive costs may be outweighed by knowledge of stable, year-round resources (ant nests) and are potentially facilitated by daily torpor or physiological gut adaptations. Dietary comparisons revealed similarities between the diets of *S. psammophila* and *S. hirtipes*, however, *S. dolichura* consumed comparatively larger prey. In summary, resource-rich dune slope habitats must be protected as a priority. Long unburned, dense lower stratum habitats appear essential to reduce predation risk for *S. psammophila* and sympatric arid zone species.

3.1. Introduction

3.1.1. Overview

The conservation of threatened species is often improved by using tracking methods to establish a species' home range and foraging preferences. Home range is the minimum area an animal requires to obtain sufficient resources such as food, shelter, and reproductive prospects, but excludes periods of vagrancy or exploration (Burt 1943). Body size may appear to be the most important determinate of home range size, i.e., large mammals have larger home ranges than small mammals because they have greater metabolic energy requirements and thus forage over a greater area (McNab 1963). For example, in the Kalahari Desert, wildebeest, *Connochaetes taurinus*, are highly mobile ungulates and can move up to 50 km in a day (Talbot and Talbot 1963). However, many other factors affect home range size for mammals in arid environments, including water deficiency, energy needs, poor soil conditions and dietary preferences, thus, small desert mammals can also travel long distances (Brown 1962, McNab 1963, Letnic 2001, Degen 2012). Spatial data can be limited for small desert mammals, however, improvements in tracking technologies and preferred habitat use analyses now make detailed spatial research possible (Kenward 1987, Aebischer *et al.* 1993, Tomkiewicz *et al.* 2010, Fattorini *et al.* 2014, Forin-Wiart *et al.* 2015).

Animals use a variety of strategies to forage optimally within their home ranges (Cowie 1977). Efficient patch use (foraging within high reward food patches) is a well-known adaptation of many mammals (Bowers and Dooley 1993, Ziv and Kotler 2003), and individuals often travel long distances to exploit such patches if the resource benefits outweigh the travel costs. For example, a radio tracked Tasmanian devil, *S. harrisii*, moved 50 km in one night to and from a garbage patch - a known high-reward food resource (Baker and Dickman 2018). Shifting home ranges that track resource pulses or patches - largely tracking rainfall events - are vital for many small desert mammals

(Perrin and Swanepoel 1987, Letnic. 2001, Brown and Ernest 2002, Yarnell *et al.* 2007). Conversely, many small desert mammal species have small and stable home ranges to retain knowledge of local food patches and to prevent predation, e.g., elephant shrews, the Macroscelididae, in the Kalahari Desert maintain their foraging paths and have runways that are etched into the ground (Randall 1993, Baker and Dickman 2018) and kangaroo rats, *Dipodomys* spp., often cache food within centrally located burrows and do not forage far from their location (Schroder 1979).

The trade-off between predation risk and foraging often affects the ranging behaviour of mammals (Lima *et al.* 1985). For example, desert dwelling baboons, *Papio cynocephalus ursinus*, spent less time feeding in high-risk food-rich habitats but more time feeding in low-risk, relatively food-poor habitats (Cowlshaw 1997). Predation risk is often measured with giving up density (GUD) experiments, i.e., the amount of resources animals are willing to leave behind correlates to their habitat use (Brown 1988). A high density of food remaining indicates low habitat usage and a low density of food remaining indicates high habitat usage. GUD experiments are a well-established method of quantifying optimal foraging in small desert mammals (Kotler *et al.* 1993, Brown *et al.* 1994, Bleicher and Dickman 2020). Analyses of radio tracking data can also infer habitat selection patterns by relating habitat use to availability (Aebischer *et al.* 1993, Fattorini *et al.* 2014, Zeale *et al.* 2012). Many small desert mammals probably perceive a high risk of predation in open habitats and lower risk in dense habitats or habitats with an uneven topography (Rosenzweig 1974, Kotler and Brown 1999). Hence, dense, unburned habitat patches are particularly important in arid environments. For example, the South African short-snouted elephant shrew, *Elephantulus brachyrhynchus*, prefers foraging within patches of unburned vegetation that provide cover (a likely anti-predator response), thus, confirming the importance of habitat 'islands' left behind after fire for the species' persistence (Yarnell *et al.* 2008).

Many small mammals avoid predation or the perceived risk of predation by limiting foraging during periods of increased risk, for example, during periods of high luminosity

(Kaufman and Kaufman 1982, Clarke 1983). However, some small desert mammals are not able to temporally alter their foraging behaviour and must forage constantly due to their high energetic requirements. Small mammals have a low tolerance of cold ambient temperatures due to their high surface area to body mass ratios, and many must remain active and forage frequently to ameliorate heat dissipation in cooler conditions (Degen 2012). Hence, they must use evasive techniques to avoid predation. For example, American heteromyids (kangaroo rats, kangaroo mice, pocket mice and spiny pocket mice) avoid visually hunting predators on moonlit nights by switching their activity from open microhabitats to shrub habitat (Randall 1993). Some heteromyids escape after detecting sounds made by predators or by detecting snake odours, and two kangaroo rat species deter snakes by kicking sand and foot-drumming (Randall 1993).

Sex and season can affect the foraging and ranging behaviour of desert mammals (Brown *et al.* 1994). For example, the bat-eared fox, *Otocyon megalotis*, forages nightly in the summer when diurnal ground temperatures are over 70 °C but switches to diurnal foraging in the winter when the ambient nightly temperature is -10 °C (Lourens and Nel 1990) and a northern Australian arid marsupial, the kaluta, *Dasykaluta rosamondae*, is exclusively diurnal in winter to reduce thermoregulatory foraging costs and avoid temporal overlap with predators (Pavey *et al.* 2016). Sex has a strong effect on home range size in small desert mammals globally (e.g., Tchabovsky *et al.* 2004, Pettett *et al.* 2018). In Australia, small spinifex-dwelling dasyurids, ningau, *Ningau* spp., males can move hundreds of metres per night despite their adult body mass of between 3.5-14 g and typically move much further than females (Baker and Dickman 2018). Rock/crevice-dwelling pseudantechinus, *Pseudantechinus* spp., males have larger home ranges than females and male kalutas, *D. rosamondae*, are more active and have larger home ranges than females (Baker and Dickman 2018).

In Australia, the 'islands of fertility' foraging theory (Schlesinger and Pilmanis 1998) is particularly important at a local scale as Australian deserts are amongst the most nutrient-poor deserts of the world (Baker and Dickman 2018). The islands of fertility theory states that xeric fauna species must typically take advantage of habitat islands where organic matter accumulates underneath shrubs and trees. This concentrates the biogeochemical cycle (in an otherwise unproductive landscape), hence, increases nutrient concentration. This in turn increases the local density and diversity of microorganisms and invertebrates - a vital food resource for many Australian small desert mammals which are often insectivorous (Schlesinger and Pilmanis 1998, Baker and Dickman 2018). Long-distance movements by small mammals in the Australian arid zone to exploit these islands are well documented (Dickman *et al.* 1995, Letnic 2001, Bos *et al.* 2002, Haythornthwaite and Dickman 2006, Dickman *et al.* 2011). Hence, small desert mammals in Australia often have large home ranges.

Many threatened Australian arid zone mammals persist only due to broad scale natural refugial habitats, i.e., natural habitats that permit a population of a threatened species to survive during periods of increased environmental pressure (Pavey *et al.* 2017, Young *et al.* 2017). Natural refugial habitats must mitigate current threats, for example, predation by introduced mesopredators, pastoral overexploitation or unmanaged wildfires, and have benefits such as rocky terrains, dense vegetation, species-appropriate fire histories and/or an abundance of primary resources (Young *et al.* 2017). Despite substantial research and conservation effort in Australia, populations of threatened species continue to decline, and without natural refugial habitats many more Australian mammal species would now likely be extinct (Woinarski *et al.* 2014).

3.1.2. The dietary preferences of small desert mammals

Integrating dietary and spatial research has improved our understanding of habitat use by threatened Australian mammal species. For example, radio tracking determined that the spotted-tail quoll, *Dasyurus maculatus*, and introduced predators have overlapping

ranges, but their diets and preferred foraging habitats differ (Glen and Dickman 2008). Radio tracking of the numbat, *M. fasciatus*, confirmed the importance of large home ranges and termite-rich foraging habitats within natural refugial habitats in both arid and temperate environments (Christensen *et al.* 1984, Friend 1987, Hayward *et al.* 2015). In general, mammals have diets that are affected by season, habitat, food quality, state (e.g., hunger), reproductive condition and physiology (Degen 2012). Desert mammals are often forced to consume poor quality resources to facilitate their survival; however, many species have physiological adaptations to extract comparatively more energy from food (Degen 2012). For example, the fat sand rat, *Psammomys obesus*, a gerbil species common to North Africa and the Middle East has longer gut villi and brush border surface areas than non-desert species that increases electrolyte and nutrient absorption (Buret *et al.* 1993). North American small desert mammals are largely granivorous, while the main granivores in Australia are ants (Morton 1979, Degen 2012). Only 12 out of 73 small desert mammals in Australia are granivores (mainly *Notomys* spp. and *Pseudomys* spp.) but these desert rodents can have highly flexible and omnivorous diets. For example, the diet of the spinifex hopping mouse, *N. alexis*, can be up to 50 % invertebrates and the diet of the sandy inland mouse, *P. hermannsburgensis*, can be up to 60 % invertebrates (Murray and Dickman 1994). Insectivory and carnivory are productive adaptations of small arid zone mammals as insects and meat are highly digestible and yield high energy rewards (Baker and Dickman 2018). Insectivores and carnivores are comparatively more common in Australian deserts than in global deserts as their winters are milder and invertebrates are a reliable year round resource (Morton 1979). Conversely, only two eutherian shrew genera, are endemic to North American deserts, while two species of hedgehog, *Erinaceidae* spp., two genera of Madagascan tenrec, *Tenrecidae* spp., and three shrew species, *Soricidae* spp., are endemic to African and Asian deserts that experience very cold winters (Stephenson and Racey 1993, Degen 2012).

The niche partitioning theory is central to our understanding of biodiversity and conservation and refers to the process by which natural selection drives competing species into different niches of resource use (MacArthur 1958). Effects such as competition, predation, isolation, and phenotypic indicators are interesting areas to examine in resource partitioning amongst sympatric species (Schoener 1974).

Competing *Sminthopsis* spp. (the hairy-footed dunnart, *S. hirtipes*, the little long tailed dunnart, *S. dolichura* and the Ooldea dunnart, *S. ooldea*) occur within the WAGVD range of *S. psammophila* and are typically smaller (mean adult body mass 10-20 g), while the 50-100 g brush-tailed mulgara, *D. blythi*, may compete with *S. psammophila* but prefers larger prey (vertebrates, orthopterans, and termites) and also preys on small dunnarts (Menkhorst and Knight 2001, Pavey *et al.* 2018, Baker and Dickman 2018). Foraging and long range movement data for *S. hirtipes*, *S. dolichura* and *D. blythi* suggest large home ranges (Dickman *et al.* 1995, Baker and Dickman 2018). All competing species are 'Least Concern' but are likely declining due to current threats (Baker and Dickman 2018), and have wider arid zone distributions than *S. psammophila*, however, *S. dolichura* is more southern and mesic (Menkhorst and Knight 2001). All competing species are thought to have the flexible diets that are commonly observed in dasyurids. For example, the stripe-faced dunnart, *S. macroura*, can switch to a mostly termitivorous diet when foraging within termite-rich habitats (Morton *et al.* 1983). Conversely, the lesser hairy-footed dunnart, *S. youngsoni* and *S. hirtipes*, forage within recently burned, open habitats to supplement their diets with fire-responsive seeds (Masters 1993, Letnic and Dickman 2005).

3.1.3. Foraging and dietary research for *S. psammophila*

Given the flexibility in the diets of sympatric dasyurids and the effect that diet has on ranging behaviour and habitat preferences, the nocturnal ecology of *S. psammophila* has been identified as a significant conservation biology knowledge gap to explore (Woinarski and Burbidge 2016). *Sminthopsis psammophila* can move quickly at

speeds of approximately one kmhr⁻¹ (Churchill 2001a, McLean 2015). Home range data are only available from 11 nocturnally radio tracked individuals from EP and YRR in South Australia (Churchill 2001a, 2001b). *Sminthopsis psammophila* was previously reported to have a relatively small mean 100 % minimum convex polygon (MCP) home range area of approximately eight ha (Churchill 2001a). However, this is not common for small Australian desert mammals. Churchill (2001a) proposed that the nocturnal ecology of *S. psammophila* may differ between the EP and YRR populations (~500 km apart), and the other known *S. psammophila* stronghold (~800 km west of YRR) in the WAGVD (Fig. 1-8) but this has not been investigated to date. Male *S. psammophila* are reported to be more mobile/transient than females (McLean 2015). Wider male ranging is a common seasonal phenomenon related to polygynous and polygynandrous social organisations wherein males mate with multiple females and is observed in many species worldwide (Gosling and Baker 1989, Cavallini 1996, Friend *et al.* 1997, Baker and Dickman 2018). Because of the relatively large testes size to body mass ratio (Appendix B) of reproductively active male individuals, *S. psammophila* likely has a multifemale mating strategy (Bedford *et al.* 1984, Rose *et al.* 1997) with sperm competition (Parker 1970). By ranging more widely males can potentially have access to mating opportunities with several females that have smaller home ranges covered by their larger ranges. Hence, the effect of sex and season on the ranging behaviour of *S. psammophila* were identified as important knowledge gaps to explore.

There is only one dietary study for *S. psammophila*, therefore, the species' dietary preferences are a significant knowledge gap. *Sminthopsis* spp. weighing over 20 g were thought to be successful within the arid zone due to their generalist, largely insectivorous, size-dependent, and opportunistic diets that exploit spatially and temporally unpredictable resources (Morton 1979, Morton 1982, Fisher and Dickman 1993). However, a morphological prey analysis by Churchill (2001a, 2001b) examined the dietary preferences of 11 individuals in total from the EP and YRR populations.

Ants were present in 95 % of the 37 faecal pellets sampled. Beetles, spiders, and grasshoppers were present in 95 %, 70 % and 57 % of samples, respectively. A house mouse, *Mus musculus*, and a small gecko were also consumed. Churchill (2001b) stressed that large prey items in a presence/absence analysis may be underrepresented and that small items, although present in most scats, may not contribute much to the overall food value. A contrasting linear index of food selection analysis comparing diet with pitfall trap data revealed that beetles, spiders, and grasshoppers were positively selected, and proposed that ants, termites, true bugs, other Hymenoptera and scorpions were negatively selected (Churchill 2001b). Thus, two conflicting theories regarding the consumption of ants were suggested, but no further analyses have been performed. *Sminthopsis psammophila* typically selected smaller sized prey species within each prey order, however, as the second largest dunnart species by body mass, it was previously theorised that larger prey would be preferred (Morton 1979, Morton 1982). Xeric dasyurids do not typically consume chitinous small prey such as ants as there is little physiological reward unless these items are consumed in high volumes, for example, at an ant nest (Greenslade 1984, Fisher and Dickman 1993), or the species has a specialised gut physiology to increase nutrient absorption (Buret *et al.* 1993).

3.1.4. Hypotheses and aims

Chapter 3 aims to examine the home range use and foraging preferences of *S. psammophila*, and the effect of sex, reproductive status and weather conditions on nocturnal ranging behaviour are assessed. Chapter 3 tests the hypothesis that *S. psammophila* selects foraging habitats that reduce predation risk and yield increased resources of its preferred invertebrate prey. It is predicted that *S. psammophila* must necessarily have large home ranges to move between available resource patches or islands in its generally unproductive desert environment. The diets of *S. psammophila*, *S. hirtipes* and *S. dolichura* are compared using morphological faecal pellet analyses to

test the hypothesis that there is local resource niche partitioning or differences in the dietary preferences of competing *Sminthopsis* spp. Relevant, evidence-based strategies for conserving *S. psammophila* are then proposed, particularly regarding primary resource management, the appropriate fire age and the habitat classes and structures preferred within conservation areas.

3.2. Methods

3.2.1. Study site

Individual *S. psammophila* were nocturnally tracked at eight sites (from east to west: sites 21, 14, 10, 9, 15, 7, 13, and 20) along the APA Eastern Goldfields Pipeline (EGP) and at site 11 that was located 60 km southwest of Tropicana Gold Mine (TGM) near the western terminus of the Plumridge Lakes Access Track (PLAT) (Fig. 2-1 and Appendix A). Characteristics of the study site are given in Chapter 2. Briefly, the study site has yellow to orange sand dunes and plains dominated by spinifex grasslands with open treed landscapes of marble gums, mallee, *Callitris* spp. and *Acacia* spp. Spinifex hummock grasslands are interspersed with clay and loam soil 'Mulga' habitats. Habitat classes (Table 1-1) were mapped using aerial imagery displayed by OpenStreetMap in QGIS (Fig. 3-1). The mean (\pm SD) minimum fire age within the study area was measured using historical satellite imagery in QGIS as 32 ± 12 years (range: 0-40+ years). This was limited by the age of the available imagery for the WAGVD; long unburned habitats were classed as 40+ years.

3.2.2. Trapping, tagging and habitat preferences

To investigate home range use, the foraging preferences and diet of *S. psammophila* were examined. Twenty-four individuals [15 males (M) and 9 females (F)] were captured using deep pitfall traps (>65 cm) in four reproductively active (R) seasons in September or October and three non-reproductively active seasons (nR) in March or

April between 2015 and 2018. Reproductive status was confirmed by body mass, the time of year (see Chapter 1) and by either a pouch examination (used, with pouch young or unused) or by measuring the size of the testes (Appendix B). Individuals were classed as (i) RM ($n = 9$), (ii) nRM ($n = 6$), (iii) RF ($n = 5$), and (iv) nRF ($n = 4$) (Fig. 3-1).

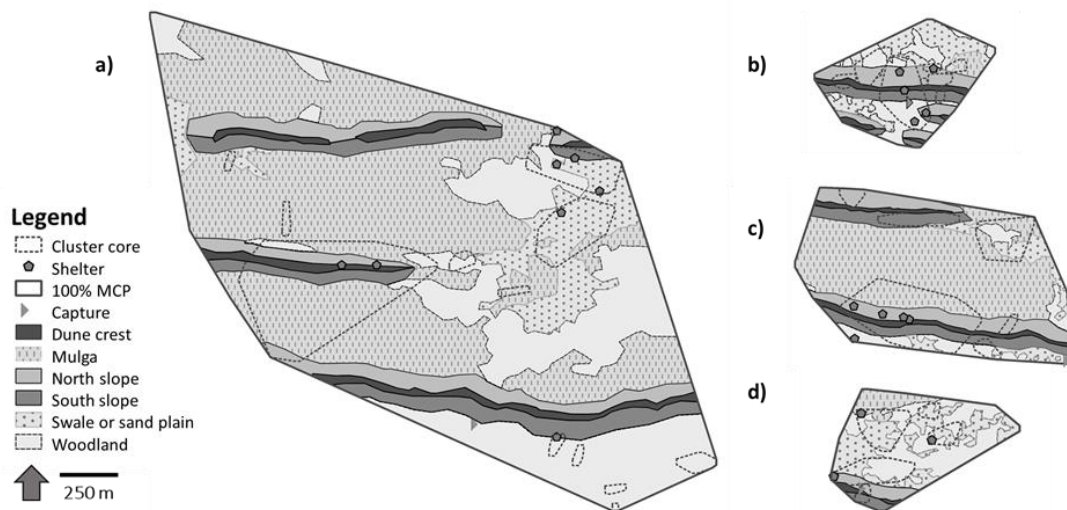


Figure 3-1. Examples of 100 % minimum convex polygon (MCP) home range areas and 90 % cluster core areas. (a) Reproductively active male (RM), (b) reproductively active female (RF), (c) non-reproductively active male (nRM), and (d) non-reproductively active female (nRF).

Trapping and tagging procedures followed Chapter 2. Individuals were tracked for three nights as 100 % minimum convex polygon (MCP) home range areas reached an asymptote after two tracking nights (an extra night was added in the event of technical issues). For individuals tracked only by radio telemetry ($n = 3$ individuals), the peak signal was recorded with a compass and the tracker's location was recorded using a Garmin eTrex GPS device. Locations were recorded every 5-10 mins from dusk to dawn using the "homing-in" method (Zeale *et al.* 2012) and by triangulating the animal's position with a second tracker. The locations of tagged individuals were calculated after field work using line-line intersection trigonometry in Excel (Microsoft Corporation 2018). Calibration triangulations were performed in the field with static tags which determined that the accuracy of radio tracking triangulation was 20 ± 2 m.

From March 2016, tagged individuals ($n = 21$) were fitted with radio transmitters attached to either a 1 g or 2 g programmable Biotrack PinPoint GPS store-on-board logger (Biotrack Ltd., Wareham, Dorset, UK) that recorded an individual's location every 10 mins between dusk and dawn with a 5-10 m accuracy. GPS logger accuracy was confirmed with static tests in known locations with a Garmin eTrex GPS device. GPS loggers recorded up to 230 locations, naturally detached and were recovered in the field using the attached radio transmitter signal. Location data were downloaded from the GPS loggers and Swift Fixes were processed using the Biotrack PinPoint Host interface on a laptop. As GPS loggers had not previously been used with small burrowing mammals, simultaneous radio and GPS tracking was performed on ten occasions. GPS logger data was highly accurate, even within shallow burrows and dense habitats, and confirmed the accuracy of radio tracking fixes. Behaviour was classified as either 'foraging' (moving signal) or 'nesting' (stationary signal). Data with less than 95 % contact time were not used for spatial analysis as the individual's behaviour and full range could not be determined. Daily sunset and sunrise times were obtained from the Bureau of Meteorology (BOM 2018), and weather data were obtained from a weather station located at TGM. Lunar illumination fraction was downloaded from the U.S. Naval Observatory (<https://aa.usno.navy.mil>). Maximum daily (sunrise to sunset) temperature ($^{\circ}\text{C}$), minimum nightly (sunset to sunrise) temperature ($^{\circ}\text{C}$), daily and monthly rainfall (mm) and moon phase as a proportion of a full moon were recorded. The effect of climatic or lunar conditions on standardised foraging times (mins), i.e. the proportion of time spent foraging within each potential nightly activity window (the time between dusk and dawn) were assessed. Cloud cover was recorded in the field and cloudy and/or rainy days (recorded by the TGM weather station) were excluded from analysis. Diurnal shelter locations were recorded using a Garmin eTrex GPS device approximately 30 minutes or more after sunrise to avoid disturbance. All further physical habitat data (e.g. habitat strata densities or number of shrubs) were determined after transmitters had detached. For ethical and license

information see Chapter 2. The individual killed by a feral cat and all faecal pellet samples were retained at the Western Australian Museum, Perth, for future study.

To investigate whether *S. psammophila* preferred certain habitat classes, location data (fixes) were analysed using Ranges 7 (Anatrack Ltd. Dorset, UK) to calculate 100 % minimum convex polygon (MCP) home range areas (ha) and 90 % cluster core areas (ha). The selection of 90 % cluster core areas was determined using a utilisation distribution discontinuity (UDD) analysis which revealed that up to 10 % of fixes increased the size of an individual's home range disproportionately (Fig. 3-2). As such, 90 % cluster core areas were considered to be a robust representation of core foraging areas (Zeale *et al.* 2012, Kenward *et al.* 2014).

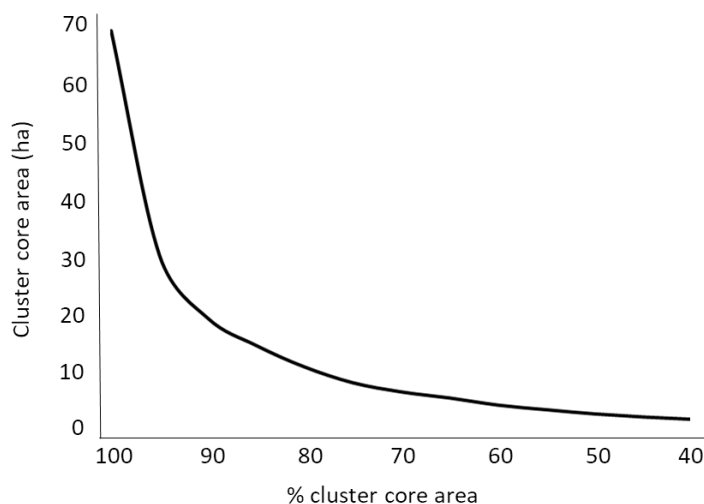


Figure 3-2. The utilisation distribution discontinuity (UDD) analysis indicated that 90 % cluster core areas were suitable for compositional analysis.

Due to spatial error in the recording of fix locations in the field, buffers of either 20 m (radio) or 10 m (GPS) were applied to an individual's fixes when calculating their MCP or cluster areas within Ranges 7. Habitat preferences were determined by comparing the habitat composition of areas used for foraging (90 % cluster core areas) with that available within home range areas (100 % MCP).

To determine if individuals preferentially foraged within habitats of a particular density, the proportions of the lower stratum (Lower) and middle stratum (Middle) available

within 25 m² plots ($n = 414$) were quantified in all habitat classes excluding 'Burned' which was not commonly used during foraging bouts (Table 1-1). Habitat strata are defined in Chapter 2 and Ground was excluded as it was previously found to be correlated with Middle. The number of shrub species (woody vegetation with several main stems arising at or near the ground; less than 2 m high) and floristic richness (the number of flora species within each plot) were determined by counting the number in each 25 m² plot.

3.2.3. Dietary preferences

Faecal pellets ($n = 210$) were collected and analysed from tracked and non-tracked *S. psammophila* ($n = 41$ individuals) between 2015 and 2018. To examine interspecific competition, faecal samples were also collected from *S. hirtipes* ($n = 12$ individuals; $n = 35$ faecal pellets) and *S. dolichura* ($n = 12$ individuals; $n = 42$ faecal pellets) and compared to those of *S. psammophila*. The diversity of each dunnart species' diet was calculated using the Brillouin index (Brillouin 1956). Data were randomised then dietary diversity was plotted against scat sample size. When the curve reached an asymptote the scat sample size was adequate to describe the diet of each dunnart species. Sex, reproductive status and biometric parameters were recorded as above for *S. psammophila*. All faecal pellets were dried and examined under a binocular microscope (7-40 \times magnification) by entomologist Dr Brian Heterick at the Western Australian Museum (WAM). Invertebrate identifications were made at species level where possible and analyses were performed at ordinal level, excluding Gastropoda, Chilopoda and Diplopoda which were identifiable to class only. Ingested hair from grooming and unidentifiable prey items were present in nearly all samples and were excluded from analyses.

3.2.4. Statistical methods

3.2.4.1. Habitat and foraging analyses

To determine habitat use, the R package *phuassess* and the means of the permutation-based combination of sign tests were used (Fattorini *et al.* 2014).

Calculation of the overall p-value (*p.overall*) determined whether proportional habitat use is demonstrated within all habitat classes. Partial p-values (*p*) and the proportion of each habitat class used (*phu.F*) were then calculated to determine if a specific habitat class was (i) preferred, (ii) used in proportion to its availability, or, (iii) avoided. A less formal ordering then ranked the habitat classes according to the preferences of *S. psammophila*.

As preliminary data indicated that RM ranges appeared much larger than all other sex/reproductive status groups (*nRM*, *RF* and *nRF*), three separate linear mixed effects (LME) models with gaussian distributions were performed to determine which fixed effects (sex and/or reproductive status) contributed most to explaining the variation observed for each response variable of (i) 100 % MCP home range area, (ii) 90 % cluster core area or (iii) maximum range span in R using the package *lme4* (Bates *et al.* 2015). The sampling units were individuals, sex and reproductive status were fixed effects and site was included as a random effect to account for pseudo-replication (Bolker *et al.* 2009). Prior to model building, data were standardised using mean and standard deviation ($(x-\mu)/\sigma$) to provide useful comparisons of effect size. To identify the most parsimonious model that explained the most amount of variance, Akaike's Information Criterion (AIC) scores for small sample sizes (AICc) were used. Pseudo R^2 ($1-(\text{residual deviance}/\text{null deviance})$) were applied to explain the fit of each model. The top four models with the lowest AICc scores were reported. For increasing precision in the calculation of estimates and associated standard errors, the model averaging approach on the final best models was applied (Burnham and Anderson 2002). The *lsmeans* package (Lenth 2017) was used to undertake post hoc contrast

tests while correcting for multiple comparisons using the Tukey method to examine differences due to sex and reproductive status.

The proportion of Lower and Middle stratum densities, the number of shrubs, and floristic richness within each habitat class [excluding 'Burned' habitats] were examined using one-way ANOVAs and post hoc Tukey tests. Pearson correlations determined whether climatic conditions (temperature, rainfall and moon phase as recorded above) had a significantly positive or negative effect on standardised foraging times.

3.2.4.2. Dietary analyses

The occurrence frequencies of prey items per scat (%FO) method expressed as a percentage the number of scats containing a prey item divided by the total number of scats collected for each individual sampled. Multivariate linear models in the R package mvabund (Wang *et al.* 2012) examined the effect of sex and reproductive status on dietary composition within *S. psammophila* and examined dietary variation between sympatric *Sminthopsis* spp. and *S. psammophila*. Sex and reproductive status or *Sminthopsis* species were used as the predictor variables and a matrix of the %FO of the 16 prey groups in each scat as the response variables, assuming multivariate normality of errors. Multivariate p-values were calculated based on 1,000 residual resamples. Non-metric multidimensional scaling (NMDS) in mvabund graphed *Sminthopsis* spp. dietary compositions. Univariate tests (either Wilcoxon rank sum tests or two sample t-tests with Bonferroni corrections) identified which prey groups differed between *Sminthopsis* spp. (Pavey *et al.* 2008, Dunlop *et al.* 2017). Dietary diversity was assessed using the %FO of the 16 prey groups as possible resource states and Levins' standardised measure of niche breadth (Levins' B) on a scale from 0 (narrow) to 1 (broad) and Levins' niche overlap ranges between 0 (no overlap) and 1 (complete overlap) were calculated (Levins 1968, Hurlbert 1978). All statistical analyses were performed in R (R Core Team and RStudio Team, 2018). Normal data are given as mean \pm SD and non-normal results as median + IQR.

3.3. Results

3.3.1. Ranging behaviour of *S. psammophila*

Twenty-four adult individuals weighing between 25 and 46 g were successfully radio and/or GPS tracked between 2015 and 2018 (Fig. 3-3). Morphometric data of individuals are given in Appendix B. *Sminthopsis psammophila* individuals were tracked for a mean of 3.1 ± 0.6 nights (range: 2-5 nights per individual) for a total of 75 tracking nights. The mean number of nightly fixes per individual was 76 ± 16 . Further tracking data including emergence times are given in Appendix B. *Sminthopsis psammophila* was active for most of the night, and the mean standardised foraging time was 97 ± 4 % (range: 79-100 %). 100 % MCP home range areas, 90 % cluster core areas and maximum range spans were highly correlated ($|R| > 0.85$ for all variable pairs). There were significant effects of sex and reproductive status on 100 % MCP home range areas, 90 % cluster core areas and maximum range spans (Tables 3-1 to 3-3). Pairwise post hoc contrast tests while correcting for multiple comparisons using the Tukey method showed a significant effect of sex for reproductively active (R) individuals (level 1 = R, level 2 = F/M, estimate = -1.51, SE = 0.30, d.f. = 16, statistic = -5.08, $p < 0.001$) but there was no effect of sex for non-reproductively active (nR) individuals (level 1 = nR, level 2 = F/M, estimate = -0.06, SE = 0.35, d.f. = 16, statistic = -0.17, $p = 0.87$).

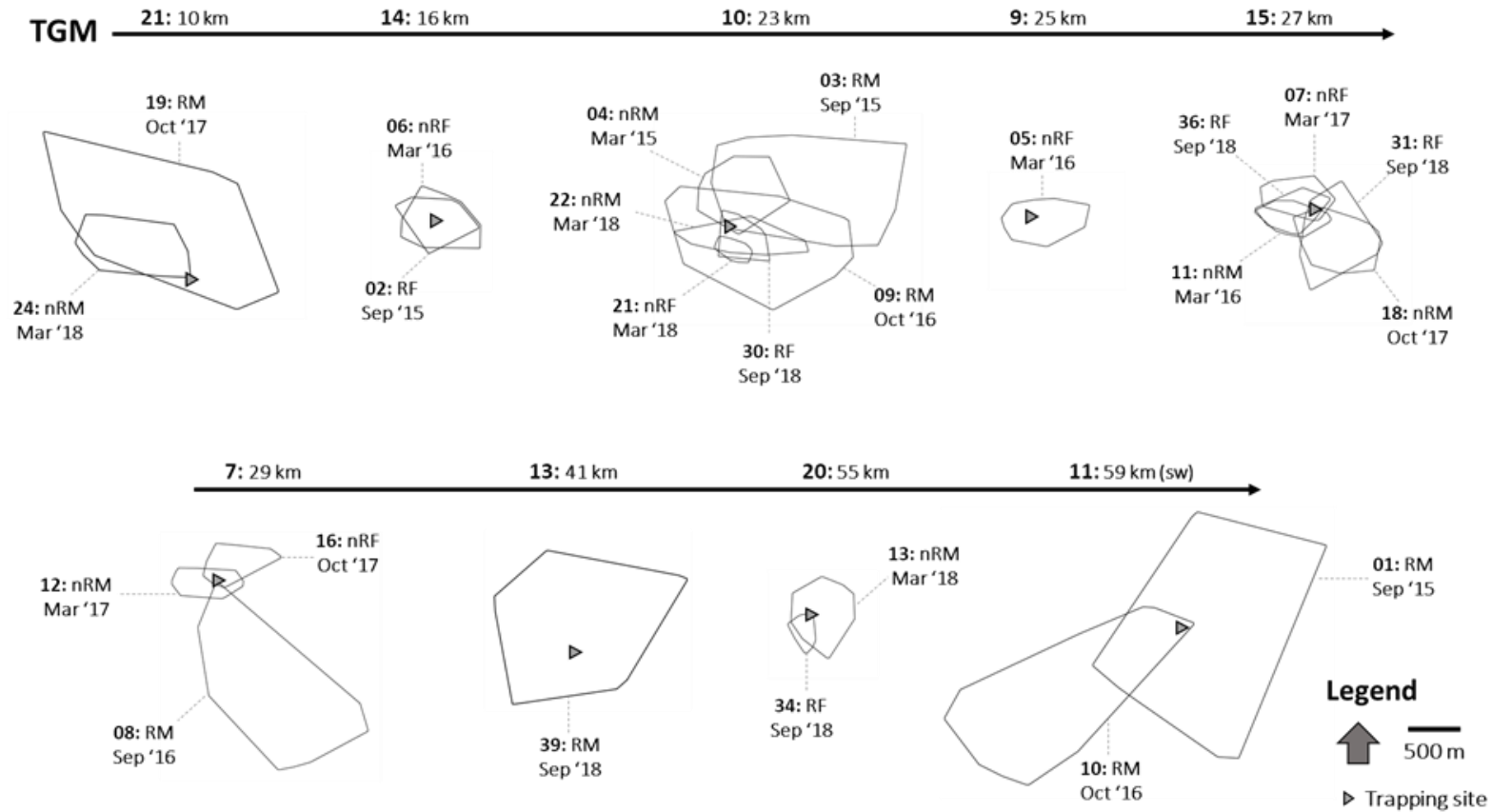


Figure 3-3. 100 % minimum convex polygon (MCP) home range areas for *S. psammophila* ($n = 24$). Site number (**bold**) and distance from Tropicana Gold Mine (TGM) are indicated above the arrow. All sites were west of TGM excluding site 11. RM = reproductively active male; nRM = non-reproductively active male; RF = reproductively active female; nRF = non-reproductively active fe

Table 3-1. Mean 100 % minimum convex polygon (MCP) home range areas (ha), 90 % cluster core areas (ha) and maximum range spans (m) for *S. psammophila*. Statistical analyses examining the differences in ranging behaviour are given in Tables 3-2 and 3-3.

Sex and status	<i>N</i>	100 % MCP home range (ha)	90 % cluster core (ha)	Maximum range span (m)
Reproductive active males (RM)	9	148 ± 73	48 ± 24	1228 ± 442
Reproductively active females (RF)	5	16 ± 7	7 ± 1	402 ± 106
Non-reproductively active males (nRM)	6	29 ± 14	10 ± 4	554 ± 142
Non-reproductively active females (nRF)	4	21 ± 11	9 ± 5	397 ± 95
<i>Sminthopsis psammophila</i>	24	70 ± 76	23 ± 24	749 ± 472

The results of LME models examining the influence of sex and/or reproductive status on the response variables of 100 % MCP home range, 90 % cluster core area and maximum range span indicated that sex contributed the most to explaining differences in the ranging behaviour of *S. psammophila* but there were no effects of reproductive status when only this effect was modelled. However, there were significant combined interaction effects of sex and reproduce status on 100 % MCP home range area, 90 % cluster core area and maximum range span (Table 3-2).

Table 3-2. 100 % MCP home range area, 90 % cluster core area and maximum range span linear mixed effects models (LME) models results indicating the effects of sex and RS on ranging behaviour. RS = reproductive status.

	Model variable	Effect size	±SE	Z	p
100 % MCP home range (ha)	Sex	1.47	0.33	4.25	< 0.001
	RS	0.01	0.38	0.02	0.98
	Sex:RS	-1.37	0.54	2.44	< 0.05
90 % cluster core (ha)	Sex	1.68	0.39	4.07	< 0.001
	RS	0.11	0.46	0.23	0.82
	Sex:RS	-1.65	0.64	2.46	< 0.05
Maximum range span (m)	Sex	1.51	0.37	3.92	< 0.001
	RS	-0.14	0.44	0.32	0.75
	Sex:RS	-1.10	0.63	1.69	< 0.01

Overall, one model performed the best (with much lower AICc scores) at explaining the differences in the ranging behaviour of *S. psammophila* for all three ranging measurements of 100 % MCP home range area, 90 % cluster core area and maximum range span (Table 3-3). The model with the lowest AICc scores used both fixed effect variables of sex and reproductive status and the interaction effect of sex and reproductive status, indicating that differences in the ranging behaviour of *S. psammophila* are explained by sex, reproductive status and the interaction of these effects.

Table 3-3. Most parsimonious and best fitting linear mixed effects (LME) models used to explain differences observed between sex and reproductive status (RS). K = the number of estimated parameters, AICc = Akaike's information criterion for small samples, Δ_i = the difference in AICc score compared to the most parsimonious model, ω_i = Akaike weights and Pseudo R^2 = the proportion of residual deviance explained by the model. Final models have been averaged.

	Model	K	AICc	Δ_i	ω_i	Pseudo R^2
100 % MCP home range (ha)	Sex + RS + Sex:RS	6	58.2	0	0.94	0.57
	Sex + RS	5	64.1	5.9	0.05	0.41
	Sex	4	69.4	11.2	0	0.19
	RS	4	69.5	11.3	0	0.15
90 % cluster core (ha)	Sex + RS + Sex:RS	6	61.8	0	0.94	0.62
	Sex + RS	5	67.9	6.1	0.04	0.45
	Sex	4	71.7	9.9	0.01	0.26
	RS	4	72.6	10.8	0	0.22
Maximum range span (m)	Sex + RS + Sex:RS	6	59.4	0	0.85	0.60
	Sex + RS	5	63.1	3.6	0.14	0.47
	Sex	4	68.1	8.7	0.01	0.27
	RS	4	71.1	11.6	0	0.16

3.3.2. Weather and moon phase results

Maximum daily temperature (mean = 28 ± 4 °C; range: 21-35 °C), minimum nightly temperature (mean = 14 ± 5 °C; range: 0-19 °C), moon fraction (mean = 0.4 ± 0.3 ; range: 0-1.0) and rainfall (mean = 0.3 ± 0.8 mm; range: 0-3.3 mm) had no statistical effect on standardised foraging times (Pearson correlations were very weak; range = -0.04-0.13). Heavy rainfall or very cold minimum ambient temperatures (0-5 °C) were infrequent (two nights) and caused prolonged nesting (30+ mins). Generally, nightly nesting times were minimal (range: 2-20 mins nightly).

3.3.3. Phuassess: habitat use of *S. psammophila*

Individuals did not use habitats in proportion to availability during nocturnal foraging (phuassess, $p_{\text{overall}} < 0.05$). 'South slope' and 'North slope' habitats were

significantly preferred over all other habitat classes, and 'Mulga' habitats were significantly avoided (Table 3-4 and Fig. 3-4).

Table 3-4. Phuassess (p.overall < 0.05) simplified ranking matrix for nocturnally tracked *S. psammophila* ($n = 24$) comparing proportions of habitats used within 90 % cluster core areas and available habitat within 100 % MCP home range areas. +++ are significant positive preferences; --- are significantly avoided; + and – indicate non-significant selection. phu.F = the proportion of habitat used for foraging overall. PREF = preferred, Prop = used proportionately, AVOID = avoided.

Habitat class	phu.F	South slope	North slope	Swale or sand plain	Dune crest	Woodland	Mulga	Decision
South slope	0.89		+	+++	+++	+++	+++	PREF
North slope	0.83	-		+++	+++	+++	+++	PREF
Swale or sand plain	0.63	---	---		+	+	+++	Prop
Dune crest	0.62	---	---	-		+	+++	Prop
Woodland	0.34	---	---	-	-		+++	Prop
Mulga	0.25	---	---	---	---	---		AVOID
Burned	0.00	(excluded from further analysis as <2 % of study site area)						

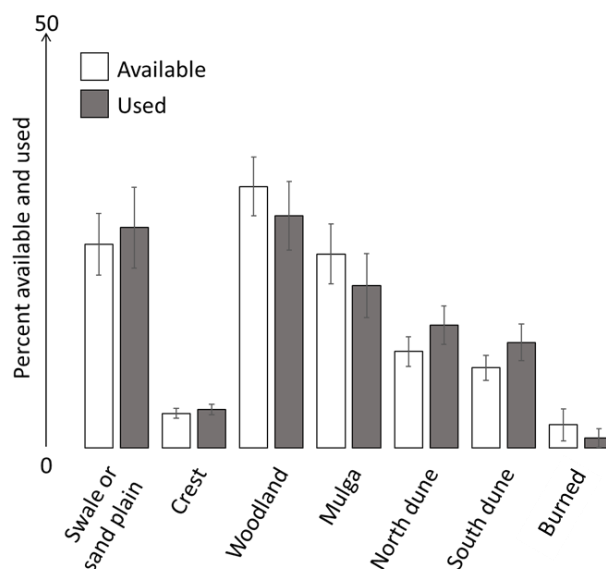


Figure 3-4. Comparisons of available habitat (100 % MCP home range area; white bars) versus habitat used (90 % cluster core area; grey bars). Mean percentage area \pm SE for *S. psammophila*.

Ranking of *S. psammophila* nocturnal foraging habitat use is as follows (>>> indicates a significant difference; > indicates non-significant): 'South slope' > 'North slope' >>> 'Swale or sand plain' > 'Crest' > 'Woodland' >>> 'Mulga' (Table 3-4). 'Burned' habitats were not typically used by *S. psammophila* during nocturnal foraging (phuasess, $\text{phu.F} = 0$) but were used on one occasion by one 46 g nRM individual during March 2018 (Fig. 2-7).

3.3.4. Habitat densities, number of shrubs and floristic richness

The proportion of Lower differed between habitat classes (one-way ANOVA, $F_{5,408} = 18.1$, $p < 0.001$). A post hoc Tukey test showed that all habitat classes excluding 'Crest' had a significantly higher proportion of Lower compared with 'Mulga' ($p < 0.001$ for all comparisons). In addition, 'South dune' had a significantly higher proportion of Lower compared with 'Crest' ($p < 0.01$); 'North slope' had a significantly higher proportion of Lower compared with 'Crest' ($p < 0.001$) and 'Woodland' ($p < 0.01$) habitats, and 'Swale or sand plain' had a significantly higher proportion of Lower compared with 'Woodland' ($p < 0.001$) and 'Crest' ($p < 0.001$) (Table 3-5).

Table 3-5. Habitat densities (proportion of ground cover) of lower stratum (Lower) and middle stratum (Middle) in the nocturnal foraging range of *S. psammophila*. See Section 2.2.3.2. for descriptions of Lower and Middle.

Habitat density variable	South slope	North slope	Swale or sand plain	Dune crest	Woodland	Mulga	Burned*
Lower	0.21 ± 0.09	0.27 ± 0.10	0.26 ± 0.14	0.15 ± 0.10	0.15 ± 0.11	0.09 ± 0.12	0.03 ± 0.02
Middle	0.22 ± 0.14	0.15 ± 0.13	0.20 ± 0.16	0.17 ± 0.13	0.18 ± 0.17	0.23 ± 0.17	0.04 ± 0.02

*Burned was excluded from analysis due to low usage by *S. psammophila* during foraging.

'South slope' habitats had a higher proportion of Middle than all habitats apart from 'Mulga', but overall Middle (mean = 0.19 ± 0.15) was not significantly different amongst habitat classes (excluding 'Burned') (one-way ANOVA, $F_{5,408} = 2.1$, $p > 0.05$) (Table 3-

5). However, the number of shrub species significantly varied between habitat classes (one-way ANOVA, $F_{5,408} = 4.8$, $p < 0.001$) (Fig. 3-5).

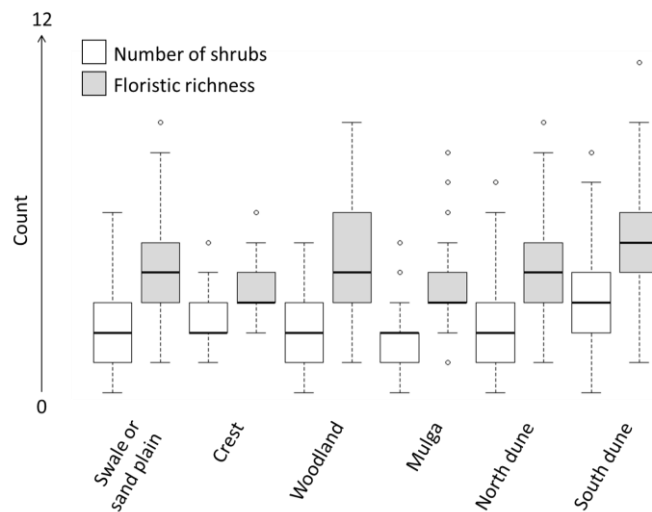


Figure 3-5. The number of shrubs \pm SE (white) and overall species richness \pm SE (grey) within habitat classes.

A post hoc Tukey test showed that 'South slope' had a significantly higher number of shrubs compared with all habitat classes: 'Crest' ($p < 0.05$), 'North slope' ($p < 0.05$), 'Swale and sand plain' ($p < 0.05$), 'Mulga' ($p < 0.001$) and 'Woodland' ($p < 0.01$).

Floristic richness was also significantly different between habitat classes (one-way ANOVA, $F_{5,408} = 4.3$, $p < 0.001$) (Fig. 3-5). A post hoc Tukey test showed that 'South slope' habitats had a higher floristic richness than 'Mulga' ($p < 0.001$), 'Swale or sand plain' ($p < 0.05$), 'Crest' ($p < 0.001$), 'North slope' ($p < 0.05$) habitat classes but not 'Woodland' ($p > 0.05$). All other comparisons were non-significant.

3.3.5. Dietary preferences

Overall, the Formicidae (ant) family accounted for 97 % of all Hymenoptera identified. Hymenoptera had the largest %FO in the diet of *S. psammophila* (Fig. 3-6). Hence, Formicidae were identified to species or genus level where possible (Appendix C). Relatively few other Hymenoptera were consumed by *S. psammophila* but this included species from the Bethyridae and Apoidea (wasp and bee) families. Other

preferred prey orders consumed at lower %FO by *S. psammophila* were Coleoptera (beetles), Hemiptera (true bugs), Chilopoda (centipedes) and Araneae (spiders).

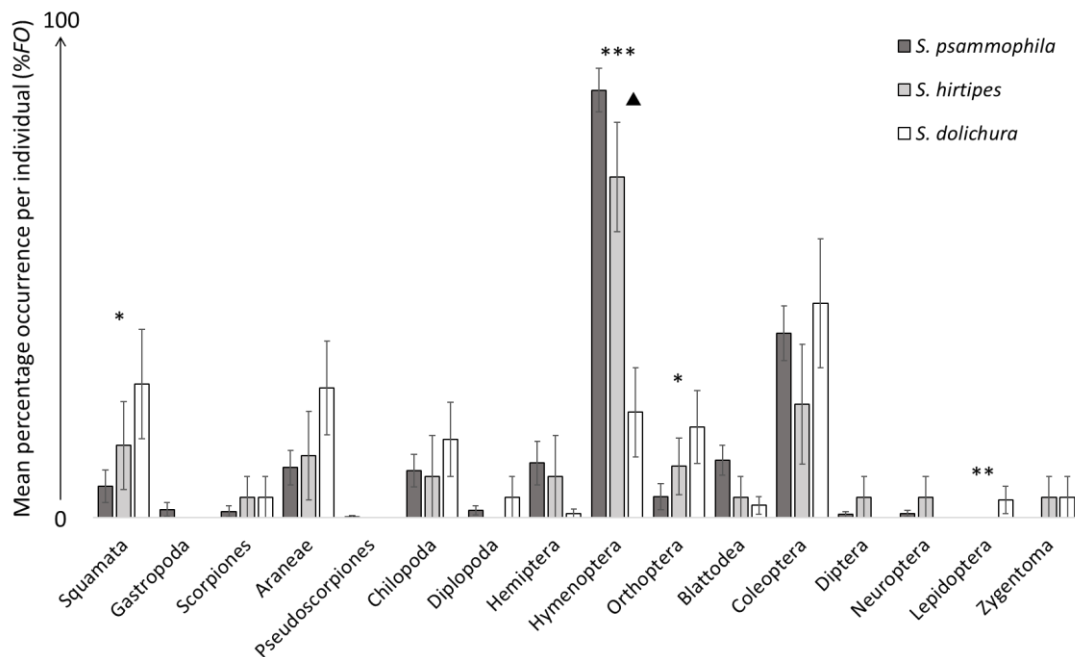


Figure 3-6. *Sminthopsis* spp. dietary preferences [percentage occurrence per individual (%FO) \pm SE]. Post hoc tests indicated significant differences between the diets of *S. psammophila* and *S. dolichura*, indicated by *** ($p < 0.001$), ** ($p < 0.01$) and * ($p < 0.05$) with Wilcoxon rank sum tests or t-tests. *Sminthopsis hirtipes* consumed significantly more Hymenoptera than *S. dolichura* ($t_{11} = 3.3$, $p < 0.01$; indicated by ▲) but no other differences in *S. hirtipes* and *S. dolichura* diet were detected (t-tests or Wilcoxon rank sum tests were non-significant).

Dietary composition was not significantly different amongst *S. psammophila* grouped by sex and reproductive status (multivariate linear modelling in mvabund, $F_{12,29} = 2.3$, $p > 0.05$). However, multivariate linear modelling and the NMDS produced in mvabund showed that dietary composition was significantly different amongst *Sminthopsis* spp. ($F_{41,24} = 4.9$, $p < 0.05$) (Fig. 3-7). *Sminthopsis psammophila* and *S. dolichura* diet differed significantly ($F_{41,12} = 4.7$, $p < 0.01$) but *S. psammophila* and *S. hirtipes* diet did not ($F_{41,12} = 1.8$, $p > 0.05$). Univariate tests showed that *S. psammophila* consumed significantly more Hymenoptera (mostly ants) than *S. dolichura* ($t_{51} = 6.9$, $p < 0.01$), but not more than *S. hirtipes* (t-test not significant, $p > 0.05$) and *S. hirtipes* also consumed significantly more Hymenoptera (mostly ants) than *S. dolichura* ($t_{22} = 3.4$, $p < 0.01$).

Larger prey items occurred significantly more frequently among samples from *S. dolichura* compared to *S. psammophila* (Wilcoxon rank sum tests: Squamata $W = 168$, $p < 0.05$; Orthoptera $W = 169$, $p < 0.05$; and, Lepidoptera $W = 205$, $p < 0.01$) (Fig. 3-7). Dietary diversity (Levins' standardised niche breadth) varied between *Sminthopsis* spp., from a minimum of 0.40 for *S. psammophila* to a maximum of 0.54 for *S. dolichura*; *S. hirtipes* standardised niche breadth was 0.51. *Sminthopsis psammophila* and *S. hirtipes* were most similar (niche overlap = 0.83) and *S. psammophila* and *S. dolichura* were least similar (niche overlap = 0.74). *Sminthopsis dolichura* and *S. hirtipes* niche overlap was 0.80.

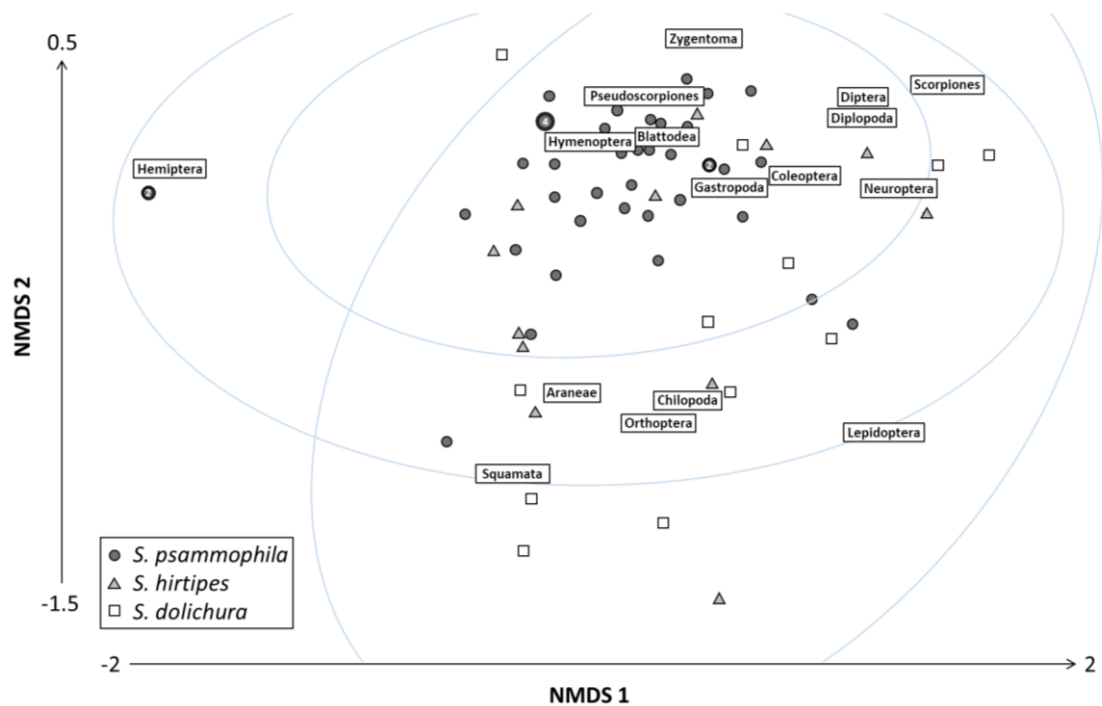


Figure 3-7. Non-metric multidimensional scaling (NMDS) of *Sminthopsis* spp. dietary composition indicating variation amongst *S. psammophila*, *S. hirtipes* and *S. dolichura*. Dietary abundance analyses used faecal pellets collected from individuals captured in the study site.

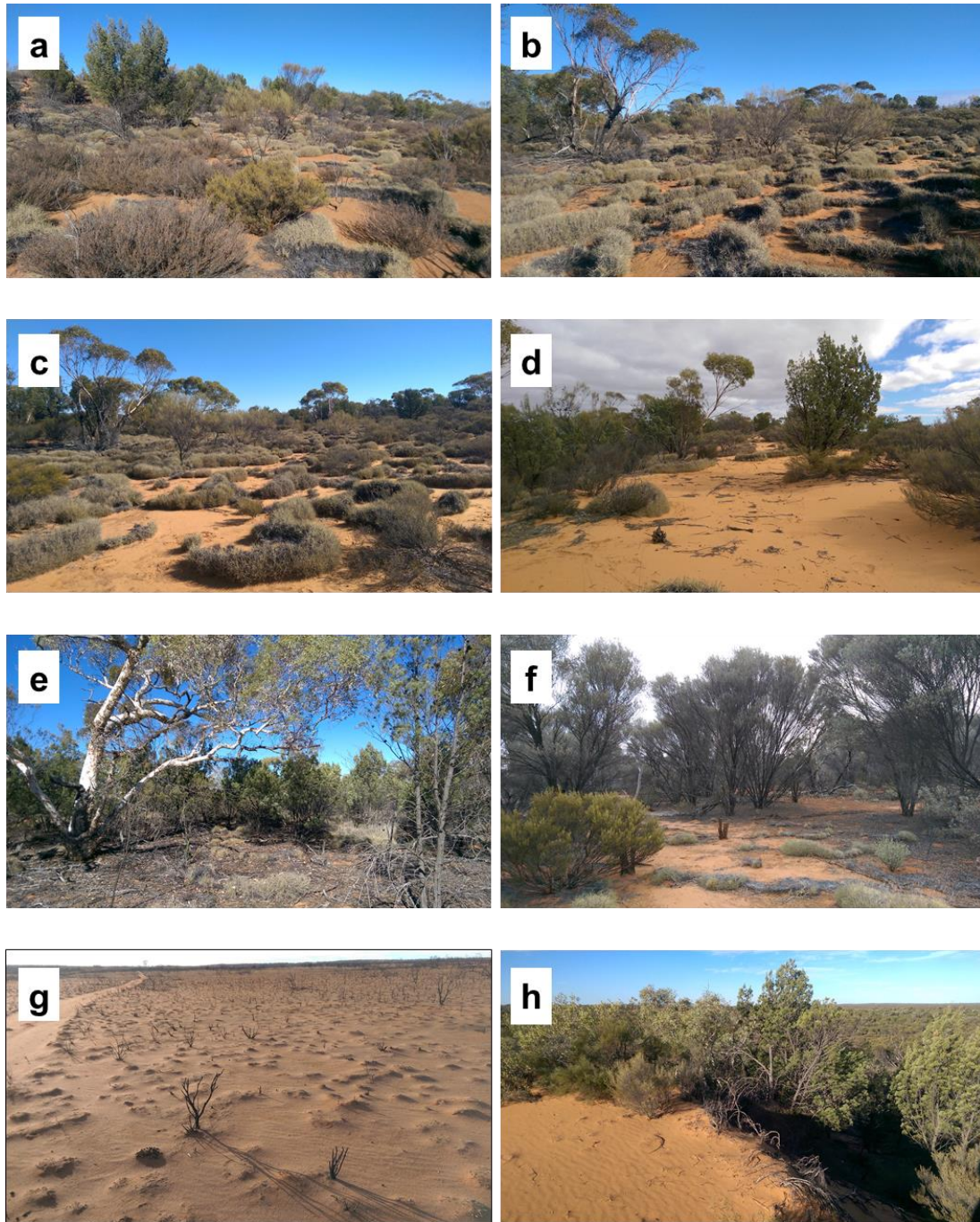


Figure 3-8. The habitat classes used by *S. psammophila* during foraging in order of preference determined by phuassess analysis (Table 3-4) were (a) South slope = PREF, (b) North slope = PREF, (c) Swale or sand plain = prop, (d) Crest = prop, (e) Woodland = prop, (f) Mulga = AVOID and (g) Burned < 2 % of total foraging habitat (excluded from phuassess analysis. (h) The difference in shade at 16:00 h on the dune crest and steep south slope. PREF = significantly selected, prop = proportionately used and AVOID = significantly avoided.

3.4. Discussion

3.4.1. Overview

Understanding how desert fauna use foraging and dietary adaptations to maximise their energy intake and avoid predation risk is important for the conservation of threatened species (Pavey *et al.* 1996, Cowlshaw 1997, Brown *et al.* 1999, Kotler and Brown 1999, Bleicher and Dickman 2020). Many factors affect small mammal ranging in arid environments, including reproduction, energy needs, heat management, and dietary preferences (Brown 1962, McNab 1963, Degen 2012). Predation risk also affects foraging behaviour, hence, dense habitats or habitats with an uneven topography are often preferred during foraging in arid environments (Laundré *et al.* 2010, Bleicher and Dickman 2020). Dense habitat patches or islands with increased richness/resources are also important to fulfil the dietary requirements of many small desert mammals. These patches can be at a local (e.g., dune slopes) or broad scale (e.g., long unburned natural refugial habitats). Small desert mammals often travel long distances to optimally forage within areas of high resource availability (Cowie 1977, Perrin and Swanepoel 1987, Letnic 2001, Brown and Ernest 2002, Letnic and Dickman 2006, Yarnell *et al.* 2007). However, the small (eight ha) home range previously reported for *S. psammophila* appears to disagree with this premise. Chapter 3 used innovative GPS tracking technologies to provide new insights into the nocturnal ecology of *S. psammophila*. Improved home range assessments and a new method for tracking small desert mammals were revealed. The importance of Formicidae (ant) prey as a stable resource for desert dwelling species is discussed and improved conservation management strategies are proposed for this poorly known desert dwelling marsupial and sympatric arid zone species.

3.4.2. The nocturnal ranging behaviour of *S. psammophila*

3.4.2.1. Home range and the effect of sex and season

The historical hypothesis that *S. psammophila* has a small home range of eight ha (Churchill 2001a) was rejected as the mean 100 % MCP home range of *S. psammophila* was 70 ha. This agrees with known ecological theory that small desert mammals, particularly in Australia, have large home ranges that maximise resource patches or islands in their unpredictable environments (Dickman *et al.* 1995, Letnic 2001, Degen 2012, Baker and Dickman 2018). Ranging data from Churchill's (2001b) unpublished study supports this finding as *S. psammophila* had a maximum home range area of 42 ha in South Australia.

There was a strong effect of sex and reproductive status on the ranging behaviour of *S. psammophila* in the WAGVD. Reproductively active females had a comparatively small mean 100 % MCP home range of 16 ha, presumably to secure or maintain breeding territories and/or good quality nesting burrows (Churchill 2001b). The 100 % MCP home range areas of all non-reproductively active individuals were between 21 and 29 ha. Conversely, reproductively active males had 100 % MCP home ranges of up to 274 ha, and two reproductively active males quickly moved beyond the team's tracking ability on foot at speeds of up to 3 kmhr⁻¹. This follows the ecological premise that reproductive state alters male ranging behaviour and that male mammals often have larger ranges than females. Extensive male ranging is widespread in mammals (Gosling and Baker 1989, Cavallini 1996, Friend *et al.* 1997, Baker and Dickman 2018) and is often related to polygynous or polyandrous social organisation. Larger reproductively active dasyurid males such as quolls and Tasmanian devils often move long distances to mate with receptive females and to defend mating territories, and there is no paternal care of offspring and multiple male fathers of each litter (Friend *et al.* 1997, Churchill 2001b, Oakwood 2002, Pavey *et al.* 2003, Glen and Dickman 2006, Baker and Dickman 2018). Hence, male *S. psammophila*, roam extensively probably to

encompass the smaller ranges of several females, giving them the potential to increase their reproductive success. It would be valuable to genotype litters to establish if males father offspring from a number of females with whom their ranges overlap. By dividing the largest reproductively active male home range area by the mean home range area of a reproductively active female, it can be inferred that an individual male may copulate with up to 17 females within its range, assuming female territories do not overlap. However, there was no evidence that female ranges do not overlap; females were caught simultaneously at several trapping sites and two females had diurnal shelters within 25 m of each other. The results of Chapter 3 suggest that protecting, maintaining and recovering large areas of natural refugial habitat are important to maintain the natural reproductive behaviour and genetic diversity of *S. psammophila*.

In the WAGVD, the 90 % cluster cores of *S. psammophila* were on average 23 ha, nearly fourfold larger than the reported mean 100 % MCP home ranges of EP and YRR *S. psammophila* (Churchill 2001b). *Sminthopsis psammophila* may have been spatially constricted in EP due to habitat fragmentation by agriculture, which may affect the species' natural ranging behaviour (Churchill 2001b). Low sample sizes (nocturnally tracked individuals: EP = 6; YRR = 5), limited location data (a mean of three fixes per 24 hours), the age of YRR individuals (subadults or juveniles) and human interference (Chapter 1) may also have affected the reported MCP home ranges for *S. psammophila* in South Australia (Churchill 2001b). Thus, it is recommended that the home range areas of South Australian *S. psammophila* are investigated further.

3.4.2.2. Resource island use

The hypothesis that *S. psammophila* proportionally uses the available habitats within its home range was rejected as 'South slope' and 'North slope' habitats were significantly preferred during nocturnal foraging. 'South slope' habitats had the highest

number of shrub species, a higher overall floristic richness and a denser middle habitat stratum compared with most other habitat classes. Therefore, the nocturnal foraging preferences of *S. psammophila* agree with the premise that habitat islands that are dense and rich in resources are important for small desert mammals globally (Brown 1988, Schlesinger and Pilmanis 1998, Stokes *et al.* 2004, Haythornthwaite 2005, Reid and Hochuli 2007, McLean 2015). For example, the spinifex hopping mouse, *N. alexis*, can travel up to three kms nightly between shrubby islands to exploit deep leaf litter, seed stockpiles and invertebrates (Dickman *et al.* 2011). Small desert mammals often have large, shifting home ranges that track resource pulses or patches, largely tracking rainfall events (Perrin and Swanepoel 1987, Letnic 2001, Brown and Ernest 2002, Yarnell *et al.* 2007). However, in the WAGVD, dune slopes are also important foraging patches due to the increased water availability of highly absorbent sandy dune soils which correspondingly increase local vegetation and invertebrate resources (Beard 1969, Alizai and Hulbert 1970, Sperry and Hacke 2002, Reid and Hochuli 2007). The topographic aspect of a dune slope can affect its sand microbiotic crust and the carbon and nitrogen content of the soil (Kidron *et al.* 2000, Yimer *et al.* 2006). In Australia, 'South slope' habitats also become shaded earlier, hence, condensation rates may be faster on southern slopes than within habitats in direct sunlight (Fig. 3-8). Consequently, dune slopes with southern aspects may have a higher water availability, nutrient content and invertebrate biodiversity. Thus, 'South slope' habitats are advantageous foraging patches for carnivorous species such as *S. psammophila*. 'North slope' habitats are likely preferred by *S. psammophila* because of the high density of lower stratum habitat that reduces predation risk and provides safe cover and "boltholes" for many sympatric small Australian desert mammals during foraging (Baker and Dickman 2018).

3.4.2.3. Behavioural adaptations and predation risk

Small desert mammals are behaviourally adapted to their arid environments in myriad ways (Brown 1962, McNab 1963, Degen 2012). For example, some small desert mammals switch from nocturnal to diurnal foraging in different seasons (Lourens and Nel 1990, Pavey *et al.* 2016). This was potentially detected for *S. psammophila* on one occasion where a 46 g non-reproductively active male was observed foraging within the hollow of a burned mallee, *Eucalyptus* sp., stump that contained a large number of ants (Fig. 2-7). The individual was startled by the researchers observing it, however, GPS tracking data then verified that the individual returned to the same hollow prior to nocturnal activity. The ambient diurnal temperature was 21 °C (this is cool for the WAGVD), hence, this individual may have been exploiting a lack of temporal competition and thermal heat stress to increase its energetic intake (Degen 2012, Pavey *et al.* 2016), despite the increased predation risk of exposure to diurnal predators. The nocturnal foraging activity of *S. psammophila* was not influenced by moon phase or weather conditions; however, extremely cold temperatures or heavy rainfall caused extended sheltering bouts. Cats, owls and other predators with large eyes, tapetum lucidum (retroreflective tissue behind the retinas) and high densities of rod (night vision) photoreceptors are extremely capable predators on dark nights (Williams *et al.* 1993, Olsen 2011). Both cats and owls have low densities of cone photoreceptors, thus, are less capable hunters in bright (day) light, however, rod photoreceptors are much more sensitive and function best in dim lights - such as moonlit nights (Williams *et al.* 1993, Olsen 2011). Hence, many small mammals reduce foraging during periods of high luminosity such as during full moons (e.g., Kaufman and Kaufman 1982, Clarke 1983). However, the visual acuity of prey, foraging efficiency and foraging habitat cover also moderate the effect of moonlight on predation risk (Prugh and Golden 2014). For example, in Argentina, Tapeti rabbits, *Sylvilagus brasiliensis*, brocket deer, *Mazama americana*, and white-eared opossums,

Didelphis albiventris, are more active on bright nights when predators are better detected visually (Huck *et al.* 2017). Similarly, the western pygmy possum, *Cercartetus concinnus*, increases activity in bright moonlight (Senior *et al.* 2020). Many small mammals are not able to temporally alter their foraging behaviour and must forage constantly due to their high energetic requirements; small mammals are comparatively less tolerant of cold temperatures and must remain active to ameliorate heat dissipation (Degen 2012). For example, light intensity has little influence on the spatial or temporal activity of the agile antechinus, *A. agilis* (Sutherland and Predavec 1999). Hence, evasive techniques are probably used by *S. psammophila* to avoid predation on moonlit nights, such as foraging near dense spinifex hummocks, detecting sounds and odours made by predators, or by using aggressive behaviours such as hissing, kicking sand and foot-drumming (Randall 1993). As two male *S. psammophila* were recorded at fast speeds of approximately 3 kmhr⁻¹, it is also likely that individuals flee rapidly when a predator is sensed (researchers had to run after tracked animals on multiple occasions during radio tracking). Typically, *S. psammophila* foraged continuously throughout the night until just before sunrise and then quickly returned to shelters that were up to one km away, another possible predator avoidance strategy. The physiological stresses of extreme cold and heavy rainfall are likely avoided by using burrows as temporary boltholes (Baker and Dickman 2018). *Sminthopsis psammophila* may also increase the length of torpor during these periods to reduce energetic costs, hence, are able to forage less and reduce energy intake on cold/wet nights (Degen 2012).

During tracking, one *S. psammophila* was killed, but not eaten ("surplus killing") by a feral cat, highlighting the threat of feral cats for *S. psammophila* and the need for feral cat control in the Great Victoria Desert (Jeff Turpin and Dr Alex Baynes, pers. comm.) (Fig. 6-2). High densities of feral cats (up to 3 per km²) were recorded by motion cameras at trapping sites and cats were consistently present over the five-year study

period. Red foxes were at low densities in the WAGVD and are more variable in numbers within the arid zone (King and Smith 1985), however, many native nocturnal predators such as owls and night birds probably also hunt *S. psammophila*.

Sminthopsis psammophila frequently crossed open habitats, e.g. the EGP track was traversed 182 times by 10 individuals between 2015 and 2018, and recently burned areas or areas of regrowth were also crossed frequently. During these periods of risky behaviour, individuals were exposed to predation pressure. Despite the constant pressure from feral cats and many other predators, *S. psammophila* capture rates were stable during the study period until a drought in 2019 (Fig. 1-3). Thus, *S. psammophila* must ameliorate predation risk using evasive strategies (e.g., Randall 1993) or by exploiting certain habitat classes that confer shelter.

The benefits of a dense lower habitat stratum of spinifex for reducing predation risk are again demonstrated by Chapter 3. Preferred foraging habitats had a mean lower stratum proportion of 0.24 ± 0.10 while avoided or unused foraging habitats had a mean lower stratum proportion of 0.06 ± 0.09 (Table 3-5). This agrees with the conclusions of Chapter 2 and supports the premise that sympatric arid zone mammals worldwide prefer habitats with a dense lower stratum that reduces predation risk (Rosenzweig 1974, Kotler and Brown 1999, Dickman *et al.* 1993, Fisher and Dickman 1993, Bos *et al.* 2002, Spirito *et al.* 2017). While invertebrate resources may be higher in 'Woodland' habitats (floristic richness was higher), spinifex growth in 'Woodland' habitats is limited due to the patchy exclusion of sunlight by the canopy and the heavily littered terrain (Johnson and Burrows 1994). However, there are often many logs within the lower stratum that may provide adequate boltholes during foraging bouts. 'Mulga' habitat classes were significantly avoided during foraging due to a sudden change in the local ecosystem, indicated by hard clay soils, a significantly less dense lower stratum and an absence of protective spinifex hummocks (Nano and Clarke 2008). 'Burned' habitats were adjacent to several home ranges but were not used by 92 % of

individuals and yielded little invertebrate prey. 'Burned' habitats are probably avoided due to the increased exposure to invasive mesopredators (McGregor *et al.* 2015, 2017) and a lack of foraging resources.

3.4.3. The dietary preferences of *S. psammophila*

The diet of small desert mammals often affects their foraging and ranging behaviour. Many desert mammals are often forced to consume poor quality resources to facilitate their survival during resource-limited conditions (Degen 2012). Generally, insectivorous desert mammals do not consume highly chitinous prey such as ants unless they have specialised behavioural, e.g., prolonged torpor within burrows to facilitate digestion (Else and Hulbert 1981, Degen 2012), or physiological, e.g., increased gut surface area (Buret *et al.* 1993), adaptations that facilitate improved nutrient absorption. Conversely, *S. psammophila* prefers an ant-rich diet but can consume a broader range of species when environmental conditions permit - this is known as "facultative dietary specialism" (Shipley *et al.* 2009). A diverse range of ants were consumed by *S. psammophila* and were often very small species (Appendix C). Nocturnal *Camponotus* spp. or "sugar ants" were commonly consumed, however, aggressive *Iridomyrmex* spp. or "meat ants" were also frequently eaten (Appendix C). Dietary preferences for ants by Australian mammals have been previously observed. For example, Abensperg-Traun and Steven (1997) confirmed that the short-beaked echidna, *Tachyglossus aculeatus*, is an ant specialist as over 50 % of its diet measured by volume comprised ants. Percentage volume in Chapter 3 was not measured due to time limitations, but the high proportion of ants in the diet of *S. psammophila* and a standardised niche breadth below '0.5' suggest that *S. psammophila* may show some signs of myrmecophage-like "facultative dietary specialism", i.e., *S. psammophila* prefers an ant-based diet but can consume a broader range of species when environmental conditions permit (Shipley *et al.* 2009). However, as *S. psammophila* consumes many other invertebrate and at least two other vertebrate prey species, and does not have

common mammalian myrmecophage characteristics, such as a long, sticky tongue or broad forelimbs, it is likely not classed as a true myrmecophage (McNab 1984). Hence, the apparent choice of an ant-based diet may be forced on *S. psammophila*, not as a preference, but because of the scarcity of other prey at certain times of the year (Shipley *et al.* 2009). Thus, an ant-based diet may be an important survival adaptation for desert fauna in the WAGVD when other invertebrate resources are scarce. In Australia's deserts, ants are abundant throughout the year, and their subterranean colonies are resistant to fire, providing a reliable, ubiquitous resource (Dr Brian Heterick, pers. comm.) Ant nests are stationary, high volume resources; hence, returning to their location(s) is beneficial when contrasted with the energy expenditure associated with random, opportunistic foraging (Abensperg-Traun and Steven 1997). Even so, ants are not commonly consumed by most Australian desert mammals (Greenslade 1984, Fisher and Dickman 1993). In contrast, reptilian ant specialists such as the thorny devil, *Moloch horridus*, are more common in Australia's deserts as reptiles can physiologically compensate against the lengthy digestion time of energetically costly, chitinous prey due to their ability to lower their metabolic rates and thus commit more energy to digestion (Else and Hulbert 1981). *Sminthopsis psammophila* demonstrates metabolic controls that may allow for an ant-rich diet, such as the ability to manipulate their basal metabolic rate with sun basking, shelter choice (Chapter 2) and selective torpor, and behavioural adaptations that increase energy intake such as diurnal foraging in favourable weather conditions were also observed (McNab 1984, Churchill 2001a, Pavey and Geiser 2008, Degen 2012). In the WAGVD, ant populations are higher and more diverse within islands of fertility, thus explaining the foraging preference of *S. psammophila* for dense and varied dune slope habitats. The broader diet of *S. dolichura* may be explained by its more mesic, southern distribution (Menkhorst and Knight 2001) which may facilitate a broader range of insect prey. Conversely, *S. psammophila* and *S. hirtipes* are mainly restricted to arid zone

distributions and may rely more upon the ubiquitous ant prey within their extreme semi-arid desert environments.

3.4.4. Limitations

Simultaneous GPS tracking of a non-reproductively active male and female revealed overlapping ranges. Overlapping ranges were also reported for EP individuals (Churchill 2001b). In the WAGVD, shelters were sometimes close to each other, but foraging was usually independent. Simultaneous tracking was only performed once as *S. psammophila* is not commonly captured; hence, further evaluation of overlapping ranges is required. This is particularly relevant to population density estimates for *S. psammophila* as overlapping territories will affect density calculations (Woinarski and Burbidge 2016). Two reproductively active males quickly moved beyond the team's tracking ability on foot at speeds of up to 3 kmhr⁻¹. Due to the logistic limitations of the study site, it was not possible to follow these males and they were not located on subsequent days, despite long searches over large areas. This suggests that reproductively active males may have even larger home ranges than recorded in Chapter 3. Future spatial research may be improved in remote desert habitats using radio tracking drones (Jiménez López and Mulero-Pázmány 2019).

Only one male *S. psammophila* was recaptured in consecutive trapping sessions between September 2015 and March 2016 at Site 11, thus demonstrating the difficulty in using mark-recapture techniques to assess population density for *S. psammophila*. The maximum distance between the male's shelter sites was 300 m, hence, the male maintained a stable home range over a period of approximately six months. In some cases, small desert mammals are sedentary to exploit known food resources, reproductive prospects or habitat patches (Baker and Dickman 2018). This again supports the theory proposed by McLean (2015) that there are both resident and transient *S. psammophila* individuals. However, the long-term (6+ months) sedentary behaviour of *S. psammophila* in the WAGVD requires further investigation.

Percentage volume is a more accurate measure of dietary preferences but was not measured due to time limitations. The hypothesis that the %FO method may underrepresent the importance of larger dietary items in the diet of *S. psammophila* was proposed by Churchill (2001b). This is a valid concern as ants were very common within the faecal pellets of *S. psammophila*, both in terms of numbers and species, but other invertebrates could not be identified with the same precision (Appendix C). Single large prey items such as Chilopoda or Orthoptera may have provided more overall gut content than many small ants, so potentially contributed more to an animal's food intake. However, the %FO analysis detected that *S. dolichura* often consumed larger prey, thus disagreeing with Churchill's (2001a) %FO hypothesis. Therefore, larger prey are likely not detected in the diet of *S. psammophila* as they are not consumed as frequently. Further clarification of the dietary preferences of *S. psammophila* may be improved using molecular methods (Zeale *et al.* 2011). This was not possible due to financial limitations; however, all faecal pellet samples are retained at the WAM for future study. To better evaluate periods of non-movement, future research is recommended to directly record *S. psammophila* activity at ant nests, potentially with thermal imaging technologies (Claridge *et al.* 2005), as some of the periods of non-movement may have included prolonged foraging bouts at ant nests.

3.4.5. Conservation management

On a broad scale, *S. psammophila* required long unburned (32+ years seral stage) and shrubby foraging habitats within dense spinifex hummock grasslands. These habitats are found within southern, semi-arid regions of the GVD and are supported by an increased volume of winter rainfall (BOM 2018). Thus, the conservation of small arid zone mammals such as *S. psammophila*, and many other species within its range, should focus on protecting large, contiguous areas of natural refugial habitats as a priority (McLean 2015, Young *et al.* 2017, Pavey *et al.* 2017, Reside *et al.* 2019). Broad-scale conservation management for *S. psammophila* is discussed further in

Chapter 4. On a local scale, dune slope habitats were preferred during foraging (Chapter 3) and swale, sand plain and dune slope habitats are required for sheltering (Chapter 2). Therefore, maintaining connectivity between these habitat classes is important. *Sminthopsis psammophila* is wide ranging at night, particularly during the reproductive season, within its limited area of occurrence. Hence, larger areas must be protected than previously thought. *Sminthopsis psammophila* requires a high proportion of ant prey; therefore, protecting, restoring and maintaining habitats that support a large volume and diversity of vegetation and invertebrate biomass are important for the species' conservation.

Wildfires are a key threat to the natural refugial habitats of *S. psammophila* because of their destruction of foraging habitats and food resources, hence, their control is urgent. Cultural burning with traditional methods has been used for many thousands of years in Australia and is particularly important for the conservation management of arid zone ecosystems to maintain an ecological balance and prevent large scale, destructive wildfires (Burbidge *et al.* 1988, Bowman 1995, Rose 1997, Bayly 1999, Moorcroft *et al.* 2012, Pascoe 2014). Hence, management strategies should focus on ecologically sustainable cultural burning to prevent large wildfires and conserve long unburned natural refugial habitats. Planning is required to perform site-specific wildfire management at optimal times of year, for example, in response to rainfall events (Driscoll *et al.* 2010, Moore *et al.* 2015).

The nocturnal foraging behaviour of *S. psammophila* suggests some natural resilience to predation risk, e.g., continuous foraging during moonlit periods. However, *S. psammophila* is within the top five non-volant, terrestrial, native mammal species with the greatest relative likelihood of being killed by feral cats (Woolley *et al.* 2019). During the study, one individual was killed but not eaten by a feral cat, demonstrating that although *S. psammophila* likely uses evasive techniques to mitigate predation risk, escape is not guaranteed. Within natural Australian landscapes, an estimated 815

million mammals per year are killed by feral cats, hence, feral cats remain a significant threat to *S. psammophila* (Murphy *et al.* 2019). Conservation measures such as feral cat baiting or deploying artificial refuges in open areas connecting key foraging habitats provide temporary safeguards for *S. psammophila* and other prey species within their range (Michael *et al.* 2004, McGregor *et al.* 2017). However, suppressing feral cat numbers often fails in the wild as cats reproduce and reinvade areas rapidly, making population control difficult without constructing exclosures (Doherty *et al.* 2015a). Unfortunately, exclosures - commonly used for protecting the habitats of threatened Australian species - may not benefit dasyurid abundance and are costly and prone to destruction by wildfire (Moseby *et al.* 2009).

As the remaining populations of *S. psammophila* are widely separated and may show ecological differences, consultations with local indigenous and scientific experts for each population (EP, YRR and WAGVD) should be made before attempting site-specific management. For example, in the WAGVD, *S. psammophila* prefers older seral stage habitats and the fast-growing and invasive buffel grass, *Cenchrus ciliaris*, may become a catastrophic threat (Marshall *et al.* 2012). Cost-effective options for *S. psammophila* in the GVD include the cessation of dingo culling [dingoes do not typically consume small mammals and eat large numbers of macropods (Johnson *et al.* 2007)] as changes in the abundance of apex predators can have up to a fourfold effect on the abundance of mesopredators (Ritchie and Johnson 2009, Smith 2015, Hunter *et al.* 2015). Conversely, reducing the impact of agriculture and habitat fragmentation may be more important for the EP population of *S. psammophila*.

3.4.6. Summary

The results of Chapter 3 support the premise that small desert mammals have specialised foraging and dietary preferences to enable their survival in arid environments. Localised resource islands or patches with a high diversity and density of shrubs were important for *S. psammophila* and support previous findings for

sympatric small desert mammals globally. Interestingly, ants were a staple dietary resource for *S. psammophila*, and further research is suggested to determine the importance of ants for other desert dwelling species. The use of GPS data loggers provided detailed insights into the nocturnal ecology of a rare, wide ranging arid zone species and has established a novel method for successfully tracking small desert mammals. Thus, *S. psammophila* is now confirmed as one of the widest ranging small mammals in the Australian arid zone, which may be due to its dietary preferences and energetic requirements. However, ranging behaviour is also strongly influenced by sex and season. While reproductively active males were very wide ranging (up to 274 ha), the mean home range of non-reproductively active individuals was still substantially larger (25 ha) than previously reported (Churchill 2001a). Hence, large, contiguous areas of shrubby, long unburned spinifex grassland habitat must be protected to provide prey items, to promote genetic diversity and to maintain natural reproductive patterns. Management recommendations on a local scale are to connect, restore and protect dune slopes, swales, and sand plains - the preferred foraging and sheltering habitats of *S. psammophila*. On a broad scale, long unburned, spinifex-dominated natural refugial habitats are important to reduce predation risk. Thus, wildfires must be managed as a conservation priority. Conversely, *S. psammophila* successfully forages during periods of high predation risk, probably by using dense habitats, burrows, and evasive techniques. Therefore, wildfire management may be the most important aspect for the conservation of *S. psammophila* and sympatric small arid zone mammals in the Australian arid zone.

Chapter 4: MaxEnt species distribution models
(SDMs) and ground-validation of model predictions
in Western Australia



Abstract

Accurately predicting the geographic distribution of *S. psammophila* is an urgent priority to improve conservation management plans. Maximum entropy (MaxEnt) species distribution models (SDMs) were used to predict the distribution of *S. psammophila* throughout Australia. Subsequently, ground-validation of the model predictions of presence and absence was performed using motion sensing cameras deployed in 163 locations in Western Australia between 2016 and 2018. Environmental variables that contributed most to the model were surface geology, the Interim Biogeographic Regionalisation for Australia (IBRA) bioregion, minimum temperature in the coldest month, mean temperature in the wettest quarter and precipitation in the wettest month. *Sminthopsis psammophila* was confirmed in 18 new locations in the WAGVD that were predicted as present by the model and was not detected in any locations predicted as absent ($n = 99$), giving the model a perfect Negative Predictive Power (NPP = 1.0) as determined by a threshold-dependent confusion matrix analysis. The model had a high Correct Classification Rate (CRR = 0.72), but a lower Positive Predictive Power (PPP = 0.28), highlighting that *S. psammophila* is difficult to detect using conventional survey techniques. Presence habitats were typically long unburned sand dune slopes, sand plains or swales that were dominated by *Triodia basedowii* and/or *T. desertorum* with a dense shrub layer. During ground-validation, an outlying population 150 km northwest of the previously known distribution of *S. psammophila* was verified by ten images on two independent cameras. Several potential conservation reserve sites were identified with a high probability of presence that are considered important strongholds for *S. psammophila*. It is recommended that priority conservation areas are actively managed against the synergistic threats of wildfires and feral mesopredators, and geographically isolated populations, such as the outlying northern WAGVD population, are monitored to detect the effects of climate change.

4.1. Introduction

4.1.1. Overview

Knowledge of the geographic distribution of a species can provide insights into the species' ecology, evolution, population size and potential responses to environmental change. However, data are often limited for threatened species that have received little research attention (e.g., Loiselle *et al.* 2003, Hending *et al.* 2020) or for taxa in remotely located regions such as deserts (e.g., Mohammadi *et al.* 2019). Species Distribution Models (SDMs) are useful for threatened species conservation management as SDMs demonstrate the importance of the environmental variables underlying a species' range while providing a robust estimation of its potential geographic distribution (Jones *et al.* 2016). SDMs can be used to infer past or future distributions, assess variations in temporal and spatial biodiversity factors or to explore niche partitioning and interspecific competition (Russo *et al.* 2016). SDMs can also focus survey work on "high-value" areas, i.e. areas with a high predicted presence for a threatened species, making field surveys better informed and cost-effective (Rebelo and Jones 2010, Russo *et al.* 2016). In addition, SDMs are beneficial for the discovery of new populations and are used globally to support a variety of conservation decisions (Guisan *et al.* 2013). A variety of SDM approaches are available for modelling species' distributions with either presence and absence, or presence-only data (Elith *et al.* 2006, Franklin 2009). Presence-only models are usually preferred for rare or remotely located species such as *S. psammophila* as true absences are difficult to confirm (Zeale 2011). Presence-only SDM methods include Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Peters 1999), Ecological Niche Factor Analysis (ENFA) (Hirzel *et al.* 2002), BIOCLIM (Busby 1986), DOMAIN (Carpenter *et al.* 1993) and MaxEnt (Phillips *et al.* 2006). However, improved biogeographic modelling methods use a multi-model approach (Franklin 2010) which links SDMs with models of species migration, landscape disturbance and succession, habitat suitability, habitat

dynamics and spatially explicit population dynamics. This approach is only feasible if the life history and habitat requirements of the threatened species is very well known - hence, it was not appropriate for the study of *S. psammophila*.

Maximum entropy (MaxEnt) is a presence-only approach to modelling species distributions that is often preferred for the conservation management of rare species with limited occurrence records, such as *S. psammophila*, as MaxEnt remains sensitive when only sparse training data are available (Guisan and Thuiller 2005, Razgour *et al.* 2011, Hending *et al.* 2020). MaxEnt consistently outperforms other model algorithms in its predictive performance and studies that ground-validate MaxEnt model predictions show that its predicted distributions are realistic (e.g., Rebelo and Jones 2010). By using a presence-only occurrence record approach, MaxEnt negates the errors produced by using SDMs that also require absence records, which are often unreliable for rare and threatened species with detection difficulties such as *S. psammophila*. MaxEnt also has a relatively simple interface with an accessible “front end” for users that are not familiar with coding or complex machine learning algorithms. See particularly Elith *et al.* (2006), Phillips *et al.* (2006) and Merow *et al.* (2013) for detailed methodologies and statistical explanations for ecologists regarding the set-up and use of the program, e.g., the correct selection of MaxEnt features or the incorporation of sampling bias files (Phillips *et al.* 2009).

4.1.2. The changing distribution of *S. psammophila*

Sminthopsis psammophila was once more widespread continentally but is now federally ‘Endangered’ and persists in just a few semi-arid, isolated populations (EPBC 1999) (Fig. 1-8). *Sminthopsis psammophila* was first recorded by Europeans in Australia’s Northern Territory during the Horn Expedition (Spencer 1896), but subsequently was presumed extinct until 1969 when individuals were captured on EP in South Australia (Aitken 1971). Individuals were then located throughout conservation reserves on EP and *S. psammophila* has also been recorded within the WAGVD and in

or near the YRR in the South Australian Great Victoria Desert (Hart and Kitchener 1986, Pearson and Robinson 1990, Copley and Kemper 1992, Way 2008, Ward *et al.* 2008) (Fig. 1-8). Recently, ancient bones (~50–500 years BP) of *S. psammophila* were verified from near Yalgoo and Lake Barlee, 400-600 km west of the recorded WAGVD population (Dr Alex Baynes, pers. comm.) indicating that *S. psammophila* was much more widespread throughout Western Australia. While surveys for *S. psammophila* have been undertaken in the location of the type specimen, *S. psammophila* has not been recorded there and so appears to be regionally extinct in the Northern Territory (Churchill 2001a). *Sminthopsis psammophila* is regarded as difficult to detect as recent targeted surveys have repeatedly failed, despite surveying within suitable spinifex habitats with deep pitfall traps (Chapter 1). The extent of remaining *S. psammophila* populations is unknown and terrestrial fauna survey effort is low due to Australia's expansive geography. Hence, providing a robust estimation of the distribution of *S. psammophila* is desirable for the species' future conservation management.

4.1.3. Hypotheses and aims

The distribution of *S. psammophila* is poorly known but the species is hypothesised to persist in “stepping-stone” populations and/or currently unknown regions within the southern semi-arid deserts of Australia. Surveys in these regions can be challenging. Hence, Chapter 4 aims to use MaxEnt SDMs to (i) predict the distribution of *S. psammophila* in Australia, (ii) identify the environmental variables that are most influential for the survival of the species, and (iii) ground-validate model predictions and test model performance. The historical difficulties regarding the detection of *S. psammophila* using conventional survey techniques are considered and conservation management strategies for *S. psammophila* are proposed regarding the species' distribution. In addition, the value of SDMs for the conservation management of rare and threatened species worldwide is discussed.

4.2. Methods

4.2.1. Study site

The distribution of *S. psammophila* was modelled throughout Australia at a resolution of 2.5 arc mins. There are two known populations of *S. psammophila* (WAGVD and YRR) in the GVD bioregion and a third population (EP) in the adjacent semi-arid habitat in South Australia (Fig. 1-8). The GVD is an important natural refugial habitat and is the largest desert in Australia (Chapter 1). It is regarded as one of the last pristine wildernesses and supports many endemic and/or threatened species of flora and fauna (Chapter 1). *Sminthopsis psammophila* habitat typically comprises semi-arid sand dunes, plains and swales that are dominated by a dense lower stratum of spinifex, *Triodia* spp., with varied and complex shrublands (Chapter 2 and Chapter 3). Hence, the modelling approach considered the habitat preferences of *S. psammophila* to select relevant environmental data which influence these ecological parameters.

4.2.2. Occurrence records

To train the model, verified species occurrence records were compiled for *S. psammophila* ($n = 51$), i.e., records were checked by experts and known to be accurate and extant (Appendix D). Only records recorded between February 1969 and December 2016 were used and records in locations where *S. psammophila* is presumed to be extinct (records prior to 1969) were excluded from the dataset. These data were sourced from a combination of the Global Biodiversity Information Facility (GBIF, www.gbif.org), the Western Australian Department of Parks and Wildlife (NatureMap 2016), the Atlas of Living Australia (ALA, www.ala.org.au) and recent field data from Western Australia (Turpin and Lloyd 2014, Vimy Resources 2015, Turpin and Riley 2017). Duplicate records within a single model grid cell (raster cell) were removed and remaining records were spatially rarefied to remove replicated records within a 10 km radius to control for spatial autocorrelation and improve model predictions (Legendre *et al.* 1993, Hernandez *et al.* 2006). A kernel density bias file

was created in SDMtoolbox (Brown 2014) and included in each model to account for uneven sampling of occurrence data across the modelling extent (Phillips *et al.* 2009).

4.2.3. MaxEnt SDM procedure

Environmental data that describe climate, topology, geology and land use were obtained from WorldClim (www.worldclim.org), Geoscience Australia (www.ga.gov.au) and the Department of Environment and Energy (www.environment.gov.au) and formatted to a resolution of 2.5 arc minutes (approximately 16 km²) in ArcGIS v.10.5.1 (ESRI Inc. Redlands, CA, USA). The extent of environmental layers comprised all of Australia. Environmental variables were tested for collinearity and highly correlated variables ($R > 0.75$) were removed prior to model building.

Table 4-1. The final environmental variables used to predict the distribution of *S. psammophila* throughout Australia in 2016 using MaxEnt species distribution models (SDMs). Cont. = continuous; Cat. = categorical. IBRA = Interim Biogeographic Regionalisation for Australia.

Variable Code	Source	Type	Description	Percent contribution (%)	Permutation importance (%)
Bio 06	www.worldclim.org	Cont.	Minimum temperature (T °C) in the coldest month	28.5	40.7
Bio 08	www.worldclim.org	Cont.	Mean temperature (T °C) in the wettest quarter	21.4	1.7
Bio 13	www.worldclim.org	Cont.	Precipitation in the wettest month (mm)	5.3	46.6
Geology	www.ga.gov.au	Cat.	Surface Geology of Australia 1M dataset 2012	35.4	4.3
IBRA	www.environment.gov.au	Cat.	IBRA 2016 subregion	9.4	6.6

Variables considered to be more ecologically relevant to *S. psammophila* were retained in favour of other correlated variables. The final set of uncorrelated environmental variables used in model building are described in Table 4-1. Categorical

variables were reclassified to 10 categories that were likely to influence habitat suitability for the species. Variables that contributed less than 1 % to model predictions were removed in a step-wise procedure. Five uncorrelated final variables remained, including Minimum temperature (T°C) in the coldest month (Bio 06), Mean temperature (T°C) in the wettest quarter (Bio 08), Precipitation in the wettest month (mm) (Bio 13), Surface Geology of Australia (Geology) and Interim Biogeographic Regionalisation for Australia (IBRA) subregion (IBRA) (Table 4-1).

SDMs were generated using MaxEnt (v.3.4.1., Phillips *et al.* 2006) and modelling procedures followed Merow *et al.* (2013). Optimal model parameters were determined by testing different combinations of regularization multiplier values (1, 1.5, 2 or 3) and model features (linear, quadratic, hinge, threshold and product), and comparing Akaike Information Criterion with a correction for small sample sizes (AICc) scores in ENMTools (Warren *et al.* 2010). The best fit model with the lowest AICc score used a regularization value of 1 and linear, quadratic, threshold, and product features. A final ten-fold cross-validated model was run using these parameters and the five environmental variables described above. Model performance was determined by threshold-independent statistical tests within MaxEnt [Area Under the Curve (AUC) of the Receiver Operating Characteristics (ROC) curve (Fielding and Bell 1997, Merow *et al.* 2013)]. A Jackknife analysis of the effect of environmental variables on training gain was generated within MaxEnt to assess their relative importance to the model (Phillips *et al.* 2006). MaxEnt probability of presence maps were converted to binary predictions for presence and absence using the threshold value that maximises the sum of sensitivity and specificity (maxSSS), which is the best thresholding method available for presence-only data (Liu *et al.* 2013). The maxSSS threshold for *S. psammophila* in areas that were predicted as present had probability of presence values ≥ 0.59 and areas that were predicted as absent had values < 0.59 .

4.2.4. Ground-validation methods

Ground-validation of the model predictions was performed between December 2016 and December 2018 using motion sensing camera traps deployed in 163 locations within the best available long unburned spinifex grassland habitats in the WAGVD, Murchison and Coolgardie bioregions (Fig. 4-1).

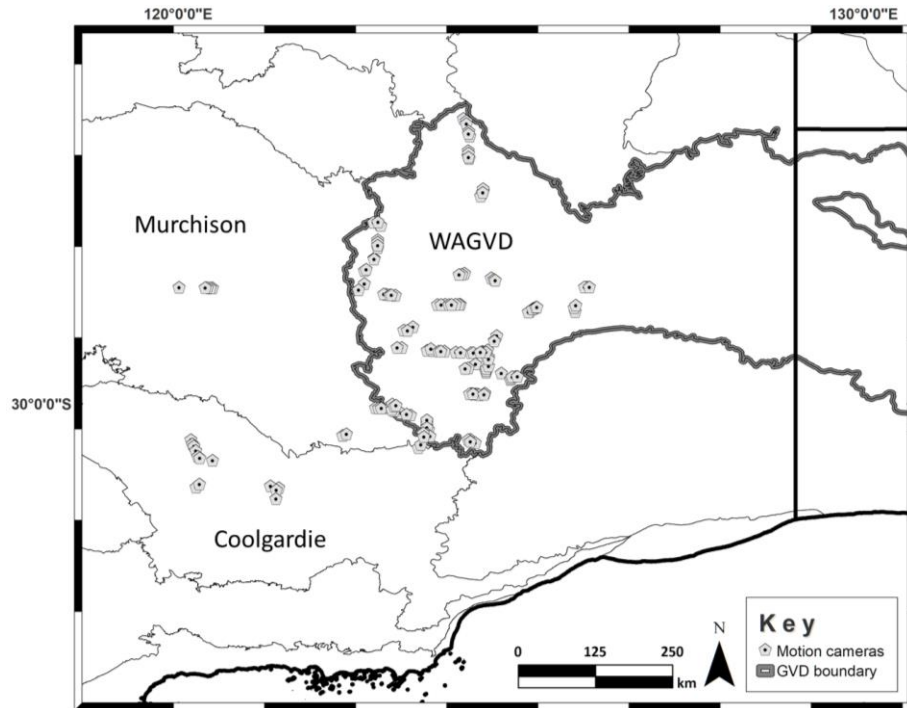


Figure 4-1. Motion-sensing camera trap locations (white pentagons with black circles) in the Western Australian Great Victoria Desert (WAGVD), Murchison and Coolgardie bioregions deployed between 2016 and 2018. State/territory borders are drawn with black lines and bioregion boundaries with grey lines [the Great Victoria Desert (GVD) bioregion is thick grey].

Sixty-four locations were in grid cells that the model predicted *S. psammophila* to be present in, while 99 locations were in predicted absence grid cells. A single camera was deployed in each grid cell for one month. More cameras were deployed in areas predicted as absent in an effort to detect *S. psammophila* outside of their known range. Cameras were baited with peanut butter, rolled oats, sardines and fish oil within anchored bait tubes. Reconyx PC900 (Holmen, WI, USA) cameras were used in 90 % of locations while Bushnell (Trophy Cam HD and Aggressor 20MP low glow, Overland Park, KS, USA), Little Acorn LTL-5610 (Oakleigh South, VIC, Australia) and

Scoutguard SG880MK-8M (Molendinar, QLD, Australia) were used in the remaining 10 % of locations. The different camera models were applied proportionately within areas predicted as present and absent to mitigate potential bias caused by differences in camera performance.

4.2.5. Confusion matrix and threshold-dependent analysis

Following ground-validation, a threshold-dependent statistical analysis assessed the predictive performance of the model based on the results of a confusion matrix (Fielding and Bell 1997) and the following performance scores:

- 1) Correct Classification Rate (CCR) = number of correctly predicted presence sites + number of correctly predicted absence sites / total number of sites
- 2) Positive Predictive Power (PPP) = number of correctly predicted presence sites / sum of correctly and incorrectly predicted presence sites
- 3) Negative Predictive Power (NPP) = number of correctly predicted absence sites / sum of correctly and incorrectly predicted absence sites

All statistical analyses were performed in R 3.5.1 (R Core Team 2018) and RStudio 1.1.463 (RStudio Team 2018).

4.3. Results

4.3.1. Model predictions

The predicted geographic distribution for *S. psammophila* based on the binary model is shown in Fig. 4-2. In Western Australia, *S. psammophila* had the highest suitability in Queen Victoria Spring Nature Reserve (QVS; $p = 0.99$). In South Australia, the Cocata Conservation Park ($p = 0.99$) and the Yumbarra Conservation Park ($p = 0.99$) were highly suitable for *S. psammophila*. Threshold-independent results were mean \pm SD cross-validated AUC training score = 0.990 ± 0.005 and AUC test score = 0.977 ± 0.0004 ; this indicated that the model possessed a high discriminative ability (Fig. 4-3).

The model predictions indicated that *S. psammophila* mostly persists within or near the current known range. However, areas of suitable climatic conditions were predicted outside of these regions, including a large area 150 km north of the known range.

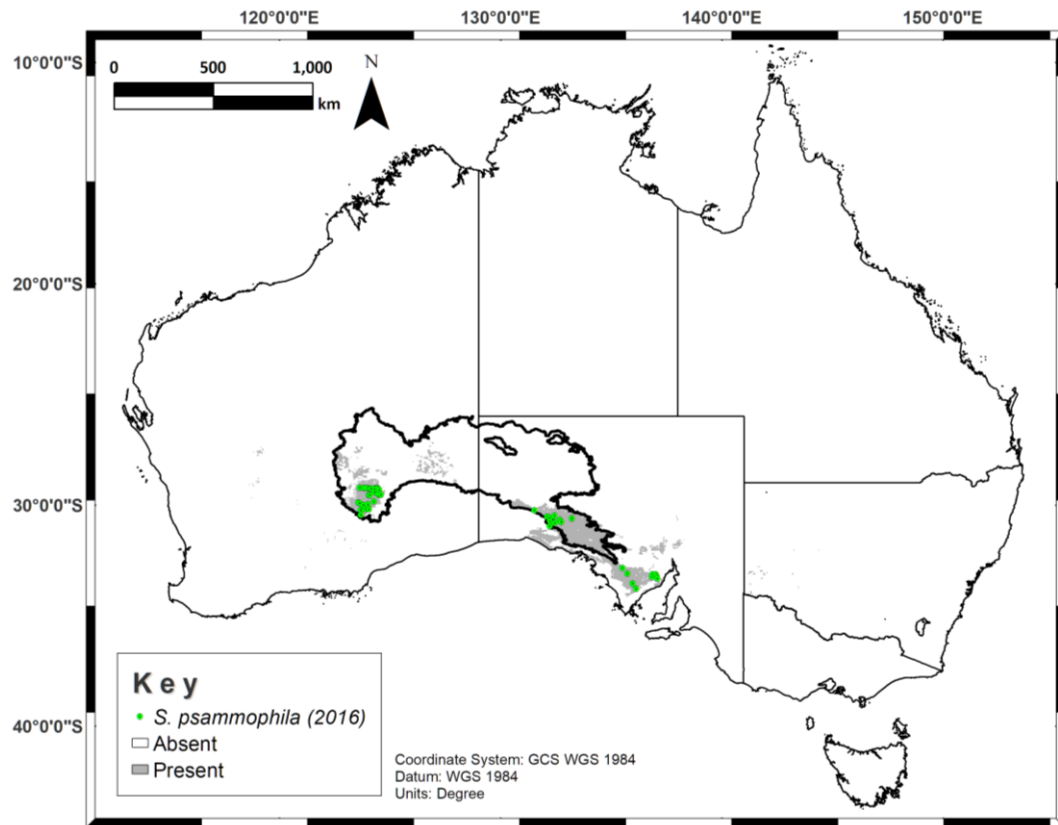


Figure 4-2. The presence (grey) and absence (white) predictions of the binary MaxEnt species distribution model (SDM) for *S. psammophila* throughout Australia. The *S. psammophila* occurrence records used for the model (light green) were compiled in 2016 (Appendix D).

4.3.2. Environmental variables

The Jackknife analysis showed that ‘Geology’ and two temperature variables (‘Bio 08’ and ‘Bio 06’) are the most informative predictors of *S. psammophila* presence, contributing 35 %, 29 % and 21 % to the model, respectively (Fig 4-3 and Table 4-1). Response curves indicated that the predicted probability of *S. psammophila* presence is highest in areas with a minimum temperature of the coldest month between 3-4 °C and a mean temperature of the wettest quarter over approximately 23 °C is not tolerated. Surface geologies of ‘Qd’ (Dunes, sandplain with dunes and swales; may

include numerous interdune claypans; may be locally Gypsiferous), 'Czs' (Sand or gravel plains; may include some residual alluvium; quartz sand sheets commonly with ferruginous pisoliths or pebbles; local clay, calcrete, laterite, silcrete, silt, colluvium) and 'Ln' (Middleback subgroup: Jaspilite; quartzite; gneiss; quartz-mica schist; dolomitic marble) are important for *S. psammophila* presence (Raymond *et al.* 2007). Response curves also indicated that several IBRA subregions within the Eyre Yorke Block and GVD bioregions and a precipitation in the wettest month of approximately 30 mm were important for *S. psammophila* presence (Fig. 4-3).

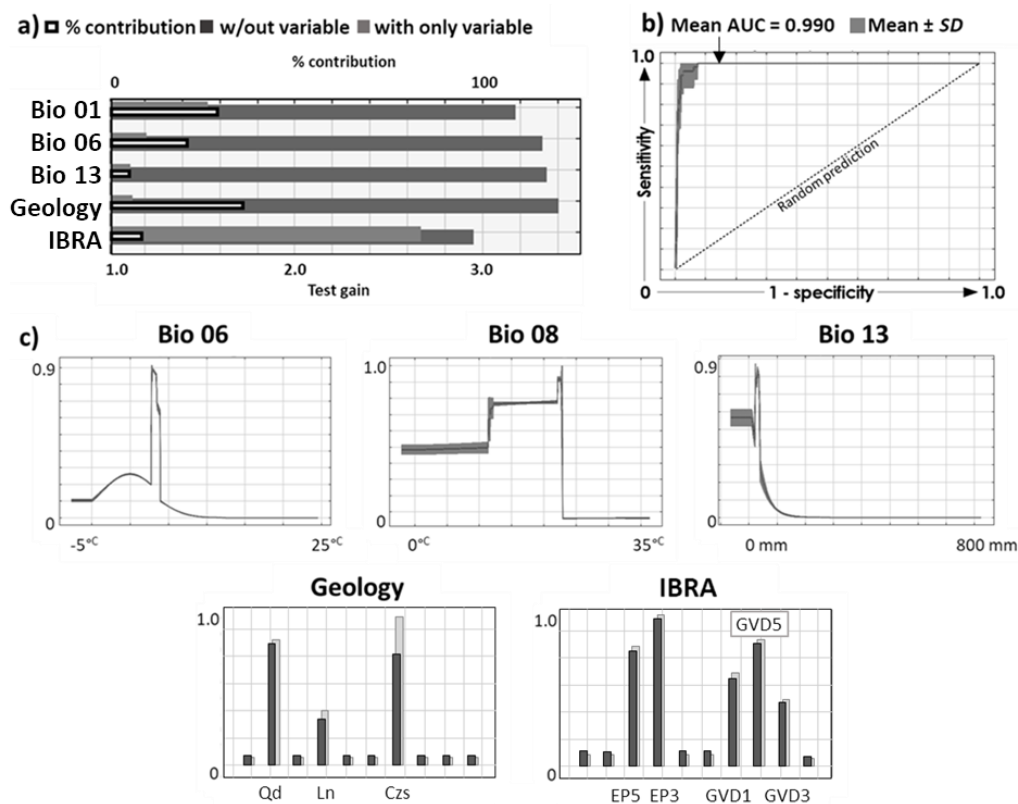


Figure 4-3. Threshold-independent statistical output. (a) The environmental variable Jackknife analysis demonstrates how each variable changed the model's gain and how the five variables contributed to modelling (variable code definitions are given in Table 4-1). (b) The ROC plot and AUC training score of 0.990 indicates that the model possesses a high predictive ability (AUC test score = 0.974) - see Section 4.2.3. for definitions of ROC and AUC. (c) The logistic output (y-axis; range: 0-1.0) response curves for environmental variables (Table 4-1) illustrated characteristics and tolerances for *S. psammophila*. Definitions of geological categories are given above. The IBRA subregions with strong response outputs were 'EP3' and 'EP5' in the Eyre Yorke Block and 'GVD1', 'GVD3' and 'GVD5' in the Great Victoria Desert (IBRA 2016).

4.3.3. Ground-validation of the MaxEnt SDM

During WAGVD ground-validation sponsored by the Goldfields Environmental Management Group (GEMG) in April 2018, *S. psammophila* was confirmed by 18 spatially independent (one per grid cell) cameras located in areas predicted as present by the model (Fig. 4-4). During GEMG ground-validation, five cameras detected *S. psammophila* in Queen Victoria Spring Nature Reserve (QVS) while ten images were captured by two cameras in a region 150 km north of the known range of *S. psammophila* (Fig. 4-5). This population was unknown previously and is a considerable range extension for *S. psammophila* in Western Australia.

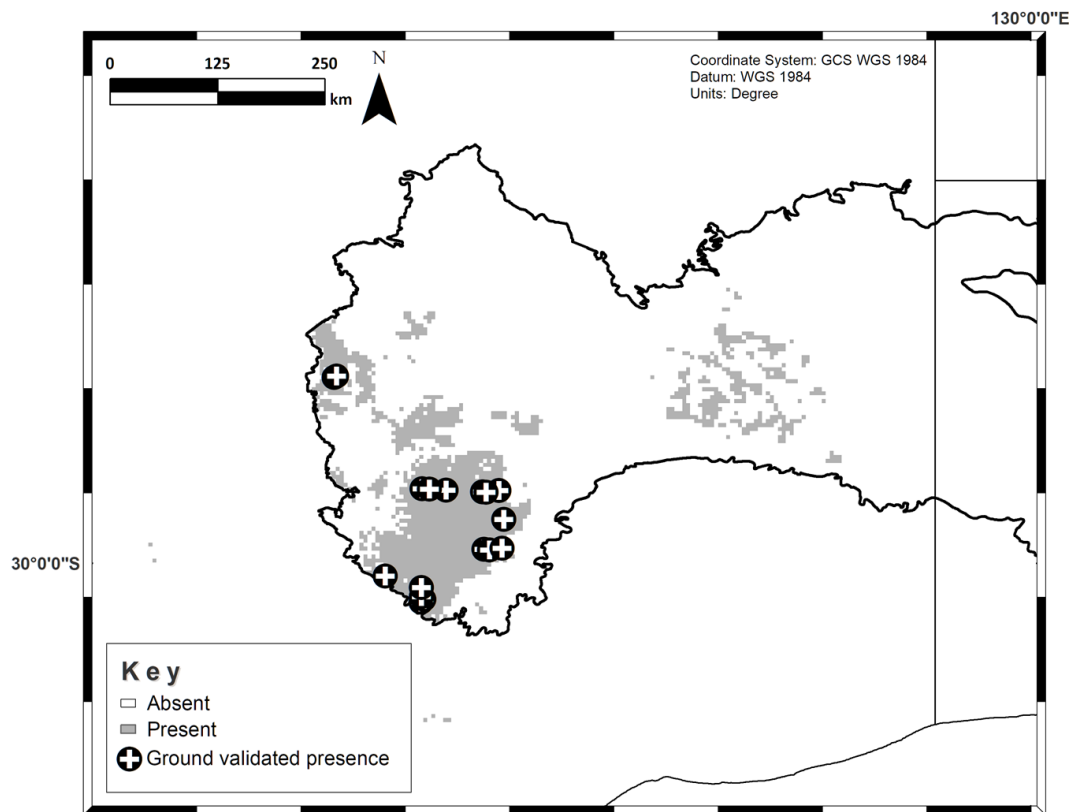


Figure 4-4. Ground-validated *S. psammophila* presences ($n = 18$, white crosses in black circles) located in the Western Australian Great Victoria Desert (WAGVD). Motion sensing camera traps ($n = 163$) were deployed for one month periods throughout the WAGVD, Murchison and Coolgardie bioregions (see Fig. 4-1 for camera trap locations). State/territory borders = thin black lines; Great Victoria Desert (GVD) bioregion = thick black line.

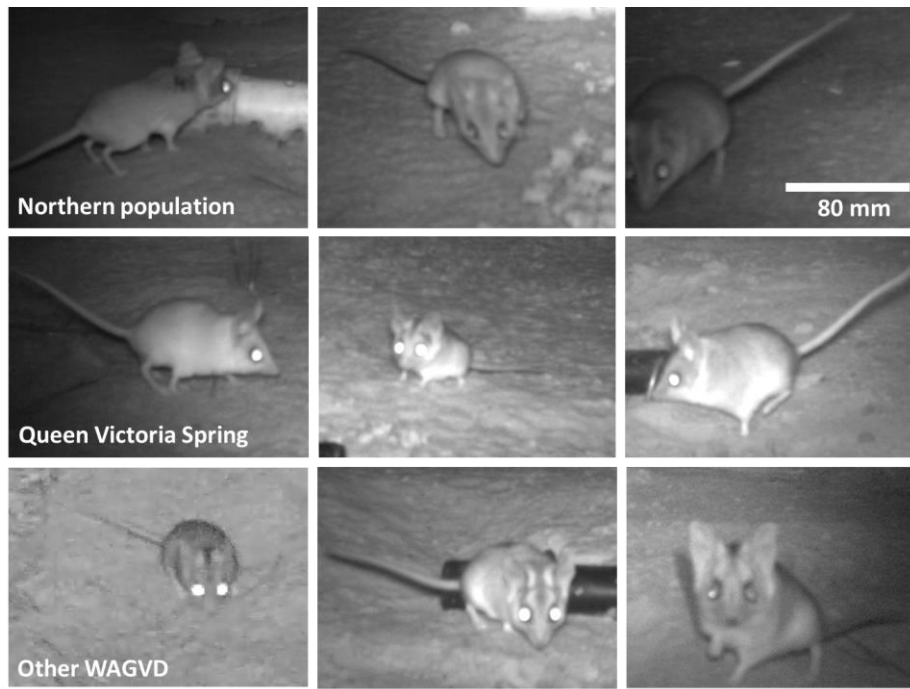


Figure 4-5. Examples of ground-validation images of *S. psammophila* captured during April 2018 [sponsored by the Goldfields Environmental Management Group (GEMG)].

The confusion matrix (Table 4-2) and threshold-dependent analysis showed that the model had a high Correct Classification Rate (CCR = 0.72) and a perfect Negative Predictive Power (NPP = 1.0), i.e., no ground-validated presences of *S. psammophila* were recorded in areas that were predicted as absent by the model (Fig. 4-6). The low Positive Predictive Power (PPP = 0.28) suggested that, although the model performed well overall, it had a greater ability to predict absences than presences.

Table 4-2. A confusion matrix (Fielding and Bell 1997) of predicted and ground-validated presences and absences used to calculate the threshold-dependent statistical analysis.

	Ground-validated presence	Ground-validated absence	Total
Predicted presence (SDM)	18	46	64
Predicted absence (SDM)	0	99	99
Total	18	145	163

All ground-validated presence records had a predicted probability of presence above the maxSSS threshold, indicating that the maxSSS threshold was an appropriate threshold to use for generating the *S. psammophila* binary models (Fig. 4-6).

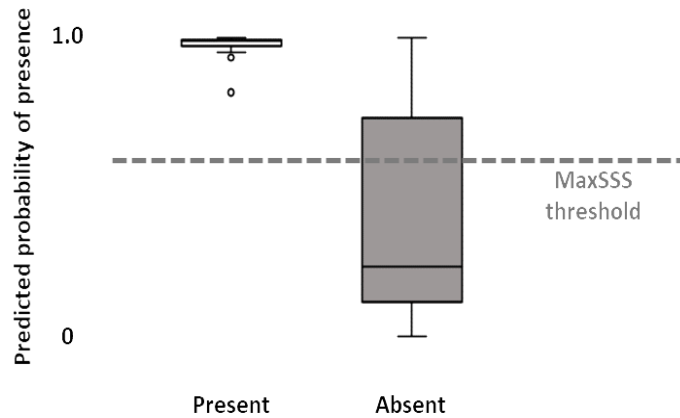


Figure 4-6. Threshold-dependent results comparing the predicted probabilities of the model (y-axis) with the present (left) and absent (right) results attained during ground-validation (x-axis). MaxSSS threshold = maximising the sum of sensitivity and specificity (Liu *et al.* 2013).

4.4. Discussion

4.4.1. Overview

Overall, the statistical output of MaxEnt demonstrated that the model performed well and in a robust manner. Hence, MaxEnt SDMs should be considered a helpful method to assist with the future conservation management of *S. psammophila*. The results of Chapter 4 support that SDMs are useful tools for the conservation management of rare and threatened species with few occurrence records. Ground-validation survey results provided confidence that the model's predictions were valid, and successfully confirmed *S. psammophila* presence in a remote region 150 km northwest of the previously known range in Western Australia. In South Australia, two *S. psammophila* records were confirmed between the EP and YRR populations in 2017 and 2020 in habitats that were predicted as present ($p = 0.98$ and $p = 0.78$) by the model (Brett Backhouse, pers. comm. and Glen Murray, pers. comm.) Throughout Australia, the

model predicts that *S. psammophila* is largely restricted to within its known range of southern semi-arid spinifex grassland habitats and is likely extinct in historical areas of occurrence such as the Northern Territory and far western Western Australia. Further ground-validation is recommended to determine the performance of the model in predicting suitable habitats in regions not yet surveyed for *S. psammophila*.

4.4.2. Environmental variables and climate

The model supports the consensus view that the distribution of *S. psammophila* is constrained by both the availability of *Triodia* spp. habitat (that is restricted to sandy soils) and a semi-arid climate. The predictions of the model were improved by using geographical and climatic environmental layers. As the ecologies of desert species are strongly influenced by climate seasonality and extremes, growing season length, stochastic rainfall and temperature variation, the current and future effects of climate change are concerning for *S. psammophila* and sympatric arid zone species (Dickman *et al.* 1995, Hughes 2003, Holmgren *et al.* 2006, IPCC 2014, McLean 2015). With the projected drying of the interior of Australia and significant changes to rainfall patterns in southern Australia, suitable conditions for *S. psammophila* are likely to be different in the near future compared to what is available for the species now. Hence, Chapter 5 uses SDMs to examine the effects of anthropogenic climate change on the future distribution of *S. psammophila* and identifies important future climatic refuges for the species' conservation.

4.4.3. Detection improvements

During ground-validation, absence predictions were easier to confirm than presence predictions (Table 4-2 and Fig. 4-6). This may be due to the population density of *S. psammophila*, which is naturally low. However, the population density of *S. psammophila* is also variable and strongly influenced by local rainfall, i.e., *S. psammophila* is harder to detect in regions that have recently experienced droughts (Masters 1993, Churchill 2001a, 2001b, McLean 2015, Turpin and Riley 2017) (Fig. 1-

3). During ground-validation surveys, the mean annual rainfall in the WAGVD region ranged from 200-400 mm (BOM 2018). Hence, an improved detection success may be attributed to healthy population densities. However, detection success was probably improved by using the updated fire age and habitat preference data for WAGVD *S. psammophila* determined in Chapter 2 and Chapter 3. Camera traps were deployed within the habitats preferred by *S. psammophila* in Western Australia, i.e., long unburned, dense spinifex grasslands and shrublands, and were not deployed in younger fire age habitats (that may be preferred in South Australia). Dense habitats are essential for the survival of many Australian mammals (Chapter 2 and Chapter 3) as they provide natural protection for prey species against predators such as the feral cat that prefer hunting in open areas (McGregor *et al.* 2015, 2017). Dense vegetation also supports a greater abundance and diversity of invertebrate fauna, thus, yielding stable prey resources for carnivorous species such as *S. psammophila* (Reid and Hochuli 2007).

4.4.4. Limitations

Due to the financial and time limitations of the project, it was not possible to perform rigorous ground-validation in South Australia. Hence, further ground-validation of the model's predictions is recommended in this region. As the risk of making false absence records is high for small, shy, nocturnal mammals, it is suggested that future ground-validation surveys are likely to produce more accurate measures for PPP if additional survey methods are used in combination with motion camera traps. For example, trained "sniffer" conservation detection dogs, nocturnal infrared cameras and environmental DNA analysis can improve the detection of rare and threatened species (Claridge *et al.* 2005, Long *et al.* 2007, Taberlet *et al.* 2012).

4.4.5. Conservation management

Within the area that was predicted as climatically and geographically suitable for *S. psammophila*, i.e., the southern and semi-arid spinifex dominated regions indicated by

Fig. 4-2 and Fig. 4-4, there is a much greater percentage reduction (90 %) in the area of habitat that is also long unburned in the WAGVD (Fig. 4-7). Due to fires in the last 20 years, much of the region will be unsuitable for *S. psammophila* from a habitat perspective.

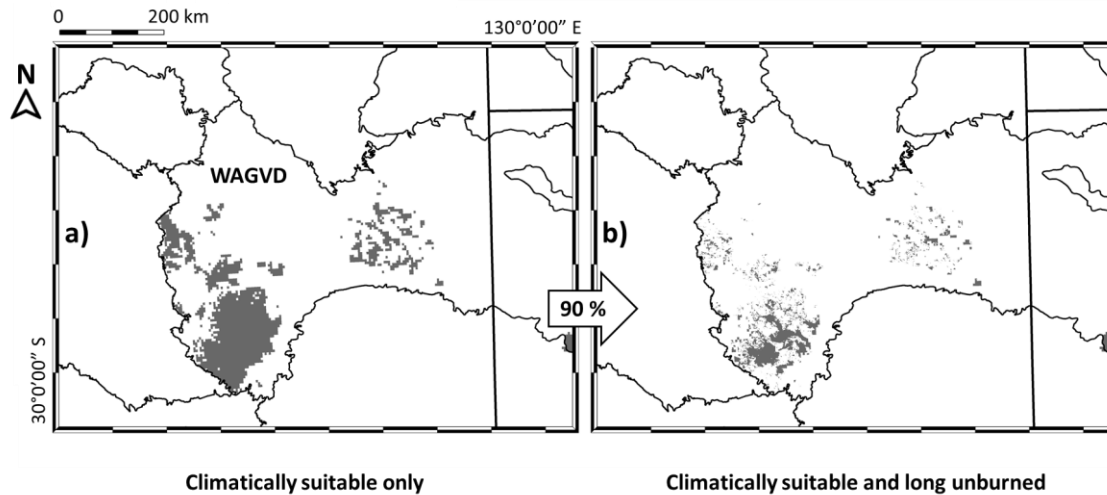


Figure 4-7. (a) The Western Australian Great Victoria Desert (WAGVD) binary MaxEnt model (grey, left) indicating climatically and geographically suitable habitat for *S. psammophila*. (b) The WAGVD binary MaxEnt model (grey, right) indicating climatically and geographically suitable and long unburned (20+ years since fire) habitat. The percentage reduction (90 %) from a) to b) in the area of suitable habitat for *S. psammophila* was calculated in ArcGIS using an intersection of annual fire scars and the binary presence model. Fire scar data were downloaded from North Australian Fire Information (NAFI; www.firenorth.org.au; GDA94 Datum). NAFI fire mapping is available for the past 20 years only. Fire scar data are not available for southern Australia.

Assuming that *S. psammophila* can persist in habitat that was burned 20+ years ago [the upper limit of fire scar data mapped by North Australian Fire Information (NAFI, www.firenorth.org.au)] the total area of climatically and geographically suitable and long unburned habitat remaining in the WAGVD was calculated in ArcGIS as 2,805 km² (Fig. 4-7 and Table 5-3). Of this, *S. psammophila* prefers only a proportion (0.43) of available habitat classes, i.e., dune slopes, swales, and sand plains (Table 1-1, Chapter 2 and Chapter 3). Hence, the total area of climatically and geographically suitable and long unburned habitat that is likely used by *S. psammophila* in the WAGVD is 1,206 km². This may be overestimated as *S. psammophila* prefers habitats

with a seral stage of 32+ years (Chapter 2 and Chapter 3). The mean home range of *S. psammophila* is 70 ha (0.7 km²). Hence, in favourable years, the population density of *S. psammophila* in the WAGVD is calculated as 1,723 individuals, meeting the IUCN Red List criteria for 'Endangered' (IUCN 2018). As resources are scarce and reproduction is costly, many desert species reproduce rapidly or "boom and bust" in response to favourable rainfall pulses that increase primary resources (Chesson *et al.* 2004, Letnic and Dickman 2006, Dickman *et al.* 2010, Thibault *et al.* 2010). Thus, small desert mammal population densities are dynamic, and in drought-affected years the population crashes. One individual was captured in the study site following a drought in 2019 compared with a mean of 10 individuals in favourable years. Hence, the drought-affected population density in the WAGVD may be as low as 172 individuals, meeting the IUCN Red List criteria for 'Critically Endangered' (IUCN 2018). These population density calculations are estimates, affected by many factors in the arid zone (Chapter 1), and are only applicable if home ranges do not overlap. As there is evidence that home ranges may overlap (Chapter 2 and Chapter 3), estimating population density for *S. psammophila* is challenging.

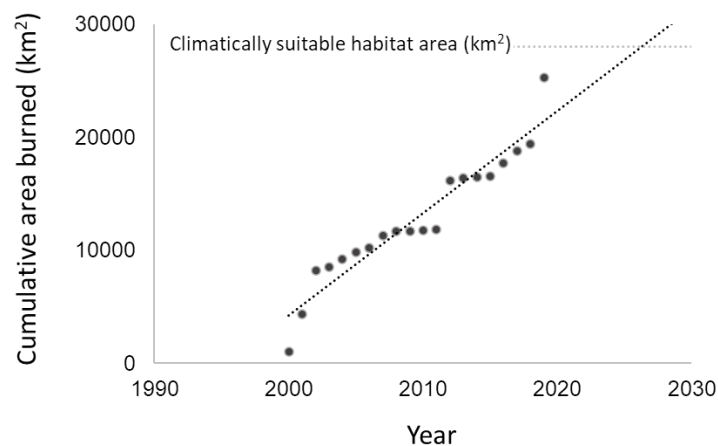


Figure 4-8. Cumulative fire scar area by year since 2000 in habitat that was predicted as climatically and geographically suitable for *S. psammophila* in the Western Australian Great Victoria Desert (WAGVD). The total area of climatically and geographically suitable habitat is indicated by the horizontal dotted line. Fire scar area data were downloaded from North Australian Fire Information (NAFI, www.firenorth.org.au).

Historical NAFI fire scar data for the past 20 years were projected assuming a linear trend ($R^2 = 0.91$) into the future (Fig. 4-8). Given the current trend, all climatically and geographically suitable habitat predicted for *S. psammophila* in the WAGVD may be burned by as early as 2026. However, the large areas that burned in 2000 and 2001 for example may recover and be suitable for *S. psammophila* again by 2020 (assuming a fire age of 20 years provides adequate spinifex habitat density and food resources to support the species). Hence, annual monitoring and fire prevention in regenerating habitats are suggested.

Recent haplotype analyses by McLean *et al.* (2018) demonstrated that, as the three known *S. psammophila* strongholds are separated both geographically and genetically, the populations of EP, YRR and WAGVD require conservation planning as distinct “Management Units” (Crandall *et al.* 2000). The results of Chapter 4 agree that there is currently no connectivity between the WAGVD and South Australian populations, hence, the conservation strategies for *S. psammophila* should be specific to the habitat requirements of each distinct population. However, there was predicted and recently verified connectivity between the EP and YRR populations, thus, these populations may share ecological adaptations. Further surveys for “stepping-stone” populations in this region are suggested. Sensitive and/or isolated populations, e.g., the northern outlying population in the WAGVD located in Chapter 4, should be monitored to detect distribution shifts. Conservation of areas with a high probability of presence of *S. psammophila* should be managed as a priority using immediate protective measures such as wildfire prevention and feral mesopredator control.

4.4.6. Summary

Chapter 4 provided insights into the geographic distribution, environmental constraints, and estimated population size of *S. psammophila*, a rare and threatened arid zone mammal. The SDMs performed well statistically, correctly predicted that *S. psammophila* should occur in 18 new locations and detected a population 150 km

north of the species' known range. However, the SDMs also indicated that *S. psammophila* is presently restricted to southern natural refugial desert habitats, hence, protecting these areas is of high conservation value for *S. psammophila* and sympatric arid zone species. This study supports the importance of including geographical variables with bioclimatic variables when predicting the distribution of species whose ranges are not exclusively constrained by climate. Overall, Chapter 4 demonstrates that SDMs can improve the conservation management of rare species and small desert mammals. The methods used can be adapted (given an informed ecological understanding of the study species in question) to improve the conservation management of rare and threatened species worldwide, and the methods can be used to project the future potential impacts of climate change (Chapter 5).

Chapter 5: Climate change and conservation planning



Abstract

Globally, the impacts of anthropogenic climate change can displace species into cooler, wetter climates. Nine of Australia's top ten warmest recorded years have occurred since 2005, and extreme events are predicted to continue to increase in frequency and/or severity in the future. Semi-arid desert specialists, such as the sandhill dunnart, *Sminthopsis psammophila*, are often dependent on winter rainfall and are susceptible to rainfall deficits, wildfires and extreme temperatures caused by anthropogenic climate change. Updated occurrence data were used to project species distribution models (SDMs) for *S. psammophila* during the mid-Holocene, present day and under two future representative concentration pathways (RCPs) of RCP 4.5 (an optimistic emissions scenario) and RCP 8.5 ("business as usual") for 2050 and 2070. By 2050 (RCP 8.5), almost all Western Australian Great Victoria Desert (WAGVD) habitat is predicted to be unsuitable for *S. psammophila*. By 2070 (RCP 8.5), the climates of the WAGVD and Yellabinna Regional Reserve populations are predicted to become unsuitable, and the species' geographic range is predicted to contract continentally by 80%. However, the 2070 (RCP 4.5) scenario wherein emissions peak in 2040 then reduce predicts that this contraction could be halved. As a semi-arid desert specialist, the distribution of *S. psammophila* is geographically limited at its southern bounds due to the cessation of suitable *Triodia* spp. habitats, and so further extension of the range southwards is not possible. Sympatric desert species may be similarly affected, thus, SDMs will be a useful tool in helping to predict the effects of climate change on their distributions.

5.1. Introduction

5.1.1. Overview

Future geographic range models are widely used to inform conservation interventions, predict species migrations, and assess the vulnerability of species to climate change (Peterson and Vieglais 2001, Beaumont and Hughes 2002, Peterson *et al.* 2002, Williams *et al.* 2003, Thuiller *et al.* 2006). For example, Thomas *et al.* (2004) used future climate change projections to predict that up to 37 % of a global sample of species may become extinct by 2050. Bakkenes *et al.* (2002) forecasted the effects of climate change on the diversity and distribution of European higher plants, demonstrating the importance of policy changes to protect geographically restrained plant communities. Species distribution models (SDMs) are increasingly popular methods to support conservation decision making (Guissan *et al.* 2013) and are often used for small mammal conservation management. For example, the current habitats of Ord's kangaroo rats, *Dipodomys ordii*, in Canada are unlikely to support the long-term persistence of populations (Heinrichs *et al.* 2010), and hence, translocations into favourable future climates may be required. SDMs are also often used for conservation management in deserts, and typically indicate future distributional shifts away from areas of increasing aridity, e.g., in South Africa, the majority of projected range shifts were in an easterly direction, reflecting the east-west aridity gradient across the country (Erasmus *et al.* 2002). Overall, future SDMs predict that most species will contract due to climate change, and support the premise that for successful global conservation, we must rapidly decrease greenhouse gas emissions and significantly increase our use of technologies such as carbon sequestration.

5.1.2. Climate change in Australia

Australia is experiencing rapid and catastrophic climate change. Annual temperatures have warmed by over 1 °C in the past century and in southwest Western Australia annual rainfall has decreased by up to 20 % (BOM 2018). As a result, Australia's

biodiversity has been negatively affected (Hoffmann *et al.* 2019). Australian species, for example, the Bramble Cay melomys, *Melomys rubicola*, Murray-Darling river fish and the Australian flying fox, *Pteropus* spp., are becoming extinct or experiencing sudden population crashes due to rising sea levels, the mismanagement of water and extreme heat events (Welbergen *et al.* 2007, Lindenmayer *et al.* 2010, Waller *et al.* 2017, Normile 2019). Most future general circulation models (GCMs) predict that we are committed to this pattern due to past emissions and that southern Australia will continue to become hotter and drier. However, the models predict that the severity of the impact of climate change on Australia's threatened species can be reduced by reducing greenhouse gas emissions (Steffen 2009, IPCC 2014, CSIRO 2017). Most recovery plans for Australia's threatened species address threats such as unmanaged wildfires, invasive species, and habitat destruction, however, climate change - an ongoing and key threatening process - is rarely confronted (Stewart *et al.* 2018). Shifts towards ecologically favourable climates have already been observed in the distribution of several Australian species, for example, the koala, *Phascolarctos cinereus*, an iconic Australian marsupial, is becoming restricted to within its southern and eastern geographical range, and it is predicted that climate change will continue to affect the geographical ranges of many species in the future (Dexter *et al.* 1995, Hughes 2003, Adams-Hosking *et al.* 2011, IPCC 2014).

Australian mammals in the arid zone have suffered rapid declines due to the displacement of the First Australians and the resulting changes in wildfire management and habitat availability and/or densities, the conversion of habitats to agriculture, industry and/or residence, competition from introduced herbivores and predation by the feral cat and the red fox (Chapter 1). However, many threatened mammals in Australia's arid zone, such as *S. psammophila*, are highly vulnerable to the rapid effects of anthropogenic climate change (McLean 2015). *Sminthopsis psammophila* is restricted to dense, southern semi-arid desert habitats (Fig. 1-8) that are influenced by

a higher winter rainfall than Australia's northern and central deserts (Chapter 4). The spinifex grassland habitats preferred by *S. psammophila* protect the species against predation but are highly flammable and therefore at an increased risk of destruction under future climate change. Uncontrolled and increasingly prevalent wildfires have repeatedly destroyed the natural refuges of *S. psammophila*, and many other Australian species, and the viability of remaining populations is unknown and terrestrial fauna survey effort is low due to Australia's expansive geography (Churchill 2001a, Woinarski and Burbidge 2016). Hence, a reliable modelling approach that assesses the impact of climate change on *S. psammophila* is required to assist with future conservation management plans. As southern Australian rainfall is predicted to decline and become increasingly irregular, there is cause for concern for the future of *S. psammophila* and many semi-arid species. Further, some models predict that in the "business as usual" future emissions scenario or RCP 8.5, Australia's annual average temperature relative to preindustrial temperatures may increase by up to 6 °C by the end of the century (Hughes 2003, Steffen 2009). This will cause significant environmental changes that many species such as *S. psammophila* may not be able to adapt to. It is therefore important to determine how ongoing climate change will affect the future distribution of *S. psammophila* and rare and/or threatened species globally.

5.1.3. Hypotheses and aims

The main hypothesis tested in Chapter 5 is that the distribution of *S. psammophila* will continue to contract because of anthropogenic climate change, which will cause significant extinction pressure on the species. As it is further north and west, the WAGVD population is hypothesised to be at a greater risk compared with other populations. Chapter 5 aims to (i) use MaxEnt SDMs to predict the past, present and future distributions of *S. psammophila* throughout Australia, (ii) verify the species' past range contraction is due to climate change using SDMs and historical occurrence records, (iii) ascertain important strongholds for *S. psammophila* under two future

emissions scenarios of a) the RCP 4.5 scenario wherein greenhouse gas emissions peak around 2040 then decline thereafter, and b) the RCP 8.5 scenario representing a “business as usual” or “worst-case” scenario - which is consistent with the current pace of global emissions - wherein emissions continue to rise throughout the 21st century. In addition, SDMs are used to propose future conservation management strategies for *S. psammophila* and sympatric threatened species.

5.2. Methods

5.2.1. Study site and species

The SDMs in Chapter 5 used updated occurrence records from Chapter 4, a modelling resolution of 2.5 arc minutes and the model bounds comprising all of Australia.

Table 5-1. All bioclimatic data and general circulation models (GCMs) were sourced from WorldClim (www.worldclim.org). All GCMs were used in the Coupled Model Intercomparison Project (CMIP5) and by the Intergovernmental Panel on Climate Change (IPCC 2014).

GCM	Modelling Centre / Group
BIOCLIM (present)	Bioclimatic variables, Ver 02, 2.5 arc minutes; Fick and Hijmans (2017)
CCSM4	National Center for Atmospheric Research
CNRM-CM5	Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancée en Calcul Scientifique
HadGEM2-CC	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)
HadGEM2-ES	
IPSL-CM5A-LR	Institut Pierre-Simon Laplace
MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies
MPI-ESM-LR/P	Max-Planck-Institut für Meteorologie (Max Planck Institute for Meteorology)
MRI-CGCM3	Meteorological Research Institute

MaxEnt SDMs and a mean of eight GCMs from the WorldClim data set (Table 5-1) predicted the present (P) distribution of *S. psammophila* and projected the distribution of *S. psammophila* during the mid-Holocene (MH) or approximately 6 ka BP. To examine the vulnerability of *S. psammophila* to future climate change, two emissions scenarios (RCP 4.5 and RCP 8.5) for 2050 and 2070 using the above GCMs were modelled. There are four commonly used future emissions scenarios (RCP 2.6, RCP 4.5, RCP 6 and RCP 8.5) that are selected for climate modelling and research, describing the different climate futures which are considered possible depending on the volume of greenhouse gases emitted during this century (IPCC 2014). The RCP 4.5 and RCP 8.5 emissions scenarios were selected as the RCP 2.6 pathway will likely be surpassed; hence, future greenhouse gas emissions will probably range between the RCP 4.5 and RCP 8.5 scenarios (depending on the scale of global greenhouse gas emissions reductions). Both 2050 and 2070 futures were modelled to support conservation management decisions for *S. psammophila*, particularly in Western Australia, where the effects of climate change are predicted to be more rapid and severe than elsewhere in Australia.

5.2.2. Modelling procedure

Bioclimatic modelling used spatially independent, verified occurrence records for *S. psammophila* ($n = 57$) recorded between February 1969 and April 2020. Occurrence data from Chapter 4 (Appendix D) were supplemented with two *S. psammophila* records confirmed between the EP and YRR populations (Brett Backhouse, pers. comm. and Glen Murray, pers. comm) and four spatially independent records determined during ground-validation in Chapter 4 from the northern outlying population, Queen Victoria Spring Nature Reserve (QVS) and near the Nippon Highway in Western Australia. The remainder of ground-validation records were within a 10 km radius of known records, hence, were not used in the climate change SDMs to control for spatial autocorrelation and to improve model predictions (Legendre *et al.*

1993, Hernandez *et al.* 2006). Environmental layer processing and GIS protocols are given in Chapter 4. To develop climate change models, bioclimatic GIS data using eight GCMs were downloaded from WorldClim (Table 5-1) and topographical data were downloaded from Geoscience Australia. Surface 'Geology' was included with bioclimatic modelling as this variable is ecologically influential for *S. psammophila*, i.e., soil type strongly influences vegetation species, structure, and density, particularly in Western Australia (Beard *et al.* 2000, Stewart *et al.* 2018). The final set of uncorrelated environmental variables used in model building is described in Table 5-2 and included 'Annual mean temperature (°C)' (Bio 01), 'Precipitation in the wettest month (mm)' (Bio 13) and 'Surface Geology of Australia' (Geology). Optimal model parameters were evaluated as per Chapter 4. The best fit model with the lowest AICc score for small sample sizes used a regularization value of '1' and 'linear, quadratic and hinge' features. A final ten-fold cross-validated model was run using these parameters and the three environmental variables described below. The categorical variable was reclassified to 10 categories that were likely to influence habitat suitability for the species.

Table 5-2. The final environmental variables with variable codes that were used for climate change modelling for *S. psammophila*. Cont. = continuous and Cat. = categorical variable.

Variable Code	Source	Type	Description	Percent contribution (%)	Permutation importance (%)
Bio 01	www.worldclim.org	Cont.	Annual mean temperature (°C)	51.7	62.0
Geology	www.ga.gov.au	Cat.	Surface Geology of Australia; 1M dataset (2012)	44.8	35.3
Bio 13	www.worldclim.org	Cont.	Precipitation in the wettest month (mm)	3.5	2.7

5.2.3. Statistical analyses

Threshold-independent statistical testing (ROC and AUC of testing and training data, Jackknife and logistical output response curves) within MaxEnt followed Chapter 4 (Fielding and Bell 1997, Phillips *et al.* 2006, Merow *et al.* 2013). Continuous MaxEnt probability of presence maps were converted to binary predictions using the maxSSS threshold and were either present ($p \geq 0.14$) or absent ($p < 0.14$) (Liu *et al.* 2013). GCMs within each time period or emissions scenario (MH, P, 2050 RCP 4.5 and RCP 8.5; 2070 RCP 4.5 and RCP 8.5) were averaged in ArcGIS using Toolbox > Cell Statistics to produce a mean model for each scenario. The percentage decreases in the size of climatically and geographically suitable habitat for *S. psammophila* were calculated by using the binary threshold-dependent models with present or absent cell classifications calculated by each model's Attribute Table in ArcGIS.

5.3. Results

5.3.1. Summary

MaxEnt first produced continuous presence probability models on a scale of 0 to 1.0 for the past, present and future projected ranges of *S. psammophila* (Fig. 5-1). The future scenarios predicted that *S. psammophila* will continue to contract southward and eastward over the next 30-50 years. In the “business as usual” scenario (RCP 8.5), most WAGVD habitat is predicted to become unsuitable for *S. psammophila* by 2050. By 2070 (RCP 8.5), all WAGVD habitat and most YRR habitat is predicted to become unsuitable. However, if there are global greenhouse gas emissions reductions (modelled by the RCP 4.5 future scenarios), *S. psammophila* may persist within the far southern extremities of the WAGVD. For example, areas within the far south of Queen Victoria Spring Nature Reserve (QVS) may remain climatically viable for the species. In the 2070 (RCP 4.5) emissions scenario, YRR habitat is predicted to reduce but its

southern extremities remain viable. However, in the 2070 (RCP 8.5) scenario, the YRR population is severely threatened (Fig. 5-2). The EP population is predicted to contract but is identified as an important climatic refugial habitat for *S. psammophila* in both future timescales and under both emissions scenarios. Continentally, in the optimistic 2070 (RCP 4.5) emissions scenario (where greenhouse gas emissions peak in 2040 and then reduce), the predicted percentage decrease of the climatically and geographically suitable distribution of *S. psammophila* is approximately half of the 2070 (RCP 8.5) “business as usual” or worst-case emissions scenario (where no action is taken on global greenhouse gas emissions) (Fig. 5-2).

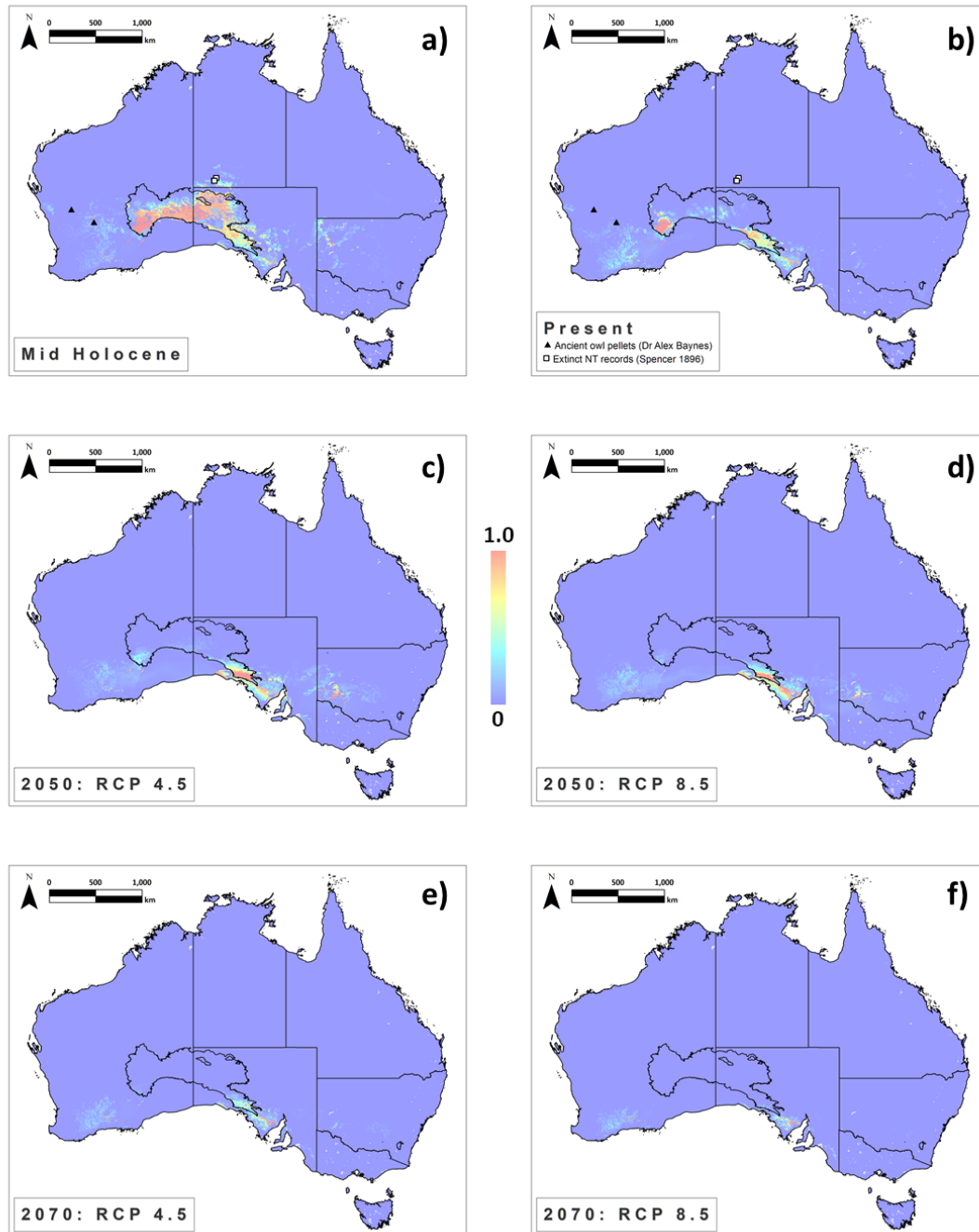


Figure 5-1. Predictions of the climatically and geographically suitable distribution for *S. psammophila* during the (a) mid-Holocene (MH), (b) present (P) and two future timescales and emissions scenarios of (c) 2050 (RCP 4.5), (d) 2050 (RCP 8.5), (e) 2070 (RCP 4.5) and (f) 2070 (RCP 8.5). The Great Victoria Desert (GVD) bioregion and state boundaries are indicated by black lines. Probability of presence is given on a continuous scale from 1.0 (red) or very likely to occur to 0 (purple) or not likely to occur. RCP = representative concentration pathway.

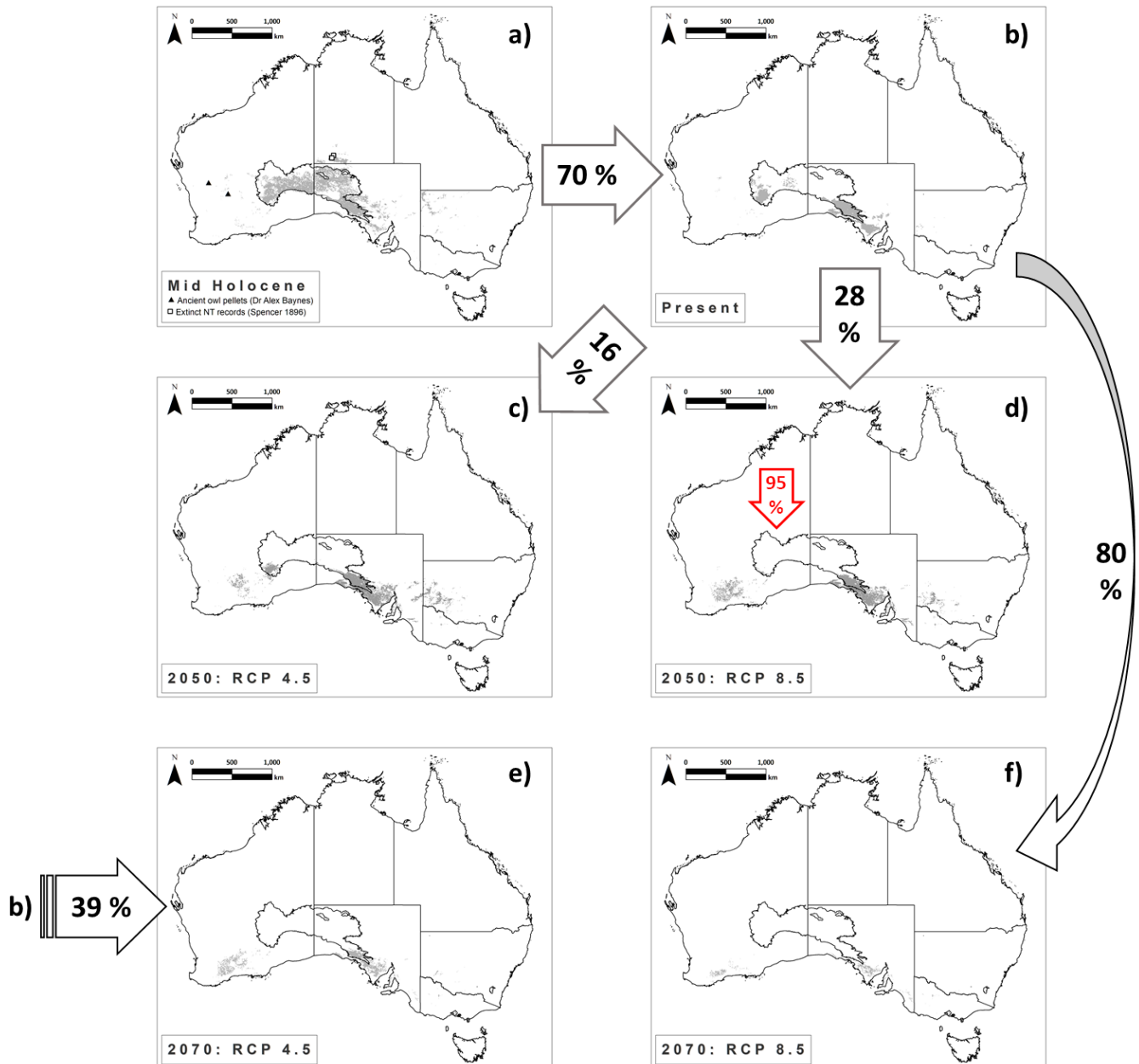


Figure 5-2. The binary predictions of *S. psammophila* presence (grey) and absence (white) during (a) mid-Holocene (MH), (b) present (P), (c) 2050 (RCP 4.5), (d) 2050 (RCP 8.5), (e) 2070 (RCP 4.5) and (f) 2070 (RCP 8.5). The Great Victoria Desert (GVD) bioregion and state boundaries are drawn with black lines. Percentage decreases in the climatically and geographically suitable areas of predicted presence for *S. psammophila* throughout Australia are indicated by black arrows. The percentage decrease for the WAGVD *S. psammophila* population only from (b) present to (d) 2050 (RCP 8.5) = 95 % (red arrow).

5.3.2. Statistical interpretation

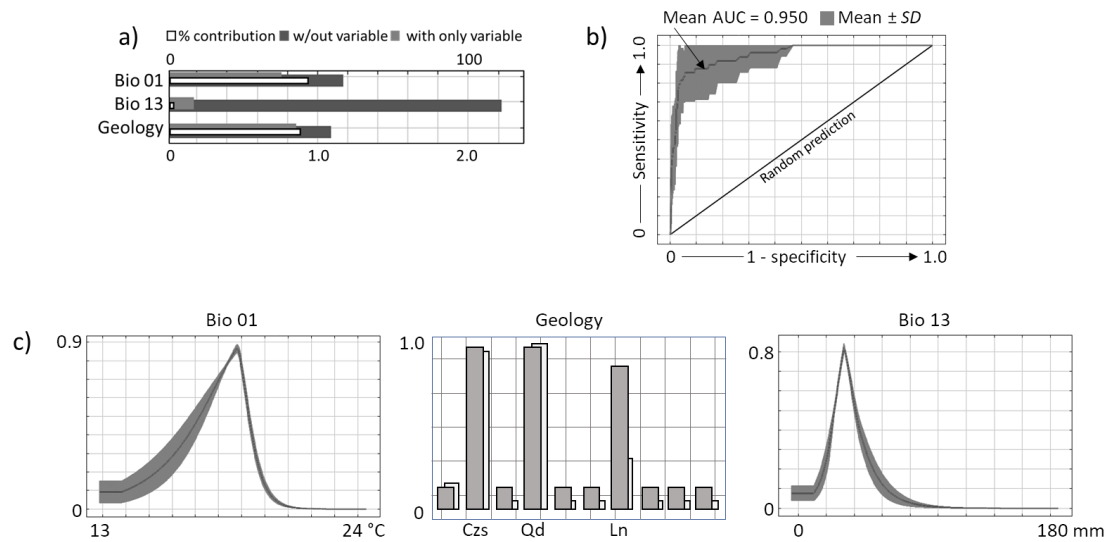


Figure 5-3. Threshold-independent statistical output indicating model performance. (a) The environmental variable Jackknife analysis demonstrated how each variable changed the model's gain and how the variables contributed to modelling. (b) The ROC plot and AUC training score of 0.967 indicates that the model possesses a high predictive ability (AUC test score = 0.950). Definitions of ROC and AUC are given in Section 4.3.2. (c) Response curves on a logistic scale (0-1.0) for environmental variables illustrated characteristics and tolerances for *S. psammophila*. Geological category definitions are given in Chapter 4. Variable codes are given in Table 5-2.

Threshold-independent results determined that the present day (P) model had a mean \pm SD AUC training score of 0.967 ± 0.006 and an AUC test score of 0.950 ± 0.049 , indicating that the model retained a high discriminative ability. The Jackknife analysis showed that 'Bio 01' and 'Geology' were the most informative predictors of *S. psammophila* presence, which contributed 52 % and 45 %, respectively, to the final model replicates (Table 5-2). The model's response curves indicated suitable conditions for *S. psammophila*, e.g., the predicted probability of presence was highest in areas with a mean annual temperature (Bio 01) of up to 19 °C, however, this declined sharply as mean annual temperature increased by as little as 1 °C (Fig. 5-3). The surface geologies that were identified as important for *S. psammophila* presence remained the same as in Chapter 4 (see Section 4.3.2 for definitions) and were 'Qd',

‘Czs’ and ‘Ln’ (Raymond *et al.* 2007). The precipitation of the wettest month (Bio 13) response curve indicated that *S. psammophila* had the highest probability of presence in regions with ~30 ml of rainfall in the wettest month.

5.4. Discussion

5.4.1. Overview

Rapid anthropogenic climate change is a key threat to many arid zone species globally (Peterson and Vieglais 2001, Beaumont and Hughes 2002, Peterson *et al.* 2002, Williams *et al.* 2003, Thuiller *et al.* 2006, Steffen 2009, IPCC 2014, McLean 2015, Arid Recovery Reserve 2019, Woinarski *et al.* 2019a). In Australia, recent and rapid climatic changes have already caused mass population crashes and extinctions (Hughes 2003, Holmgren *et al.* 2006, Welbergen *et al.* 2007, Steffen 2009, Adams-Hosking *et al.* 2011, Waller *et al.* 2017). Prioritisation to determine the level of threat (predicted future range contraction) of individual desert species is required. While Australian conservation guidelines often address key threatening processes such as invasive mesopredators, land clearing or wildfires, Australia’s rapidly changing climate is rarely discussed (Fig. 5-4).

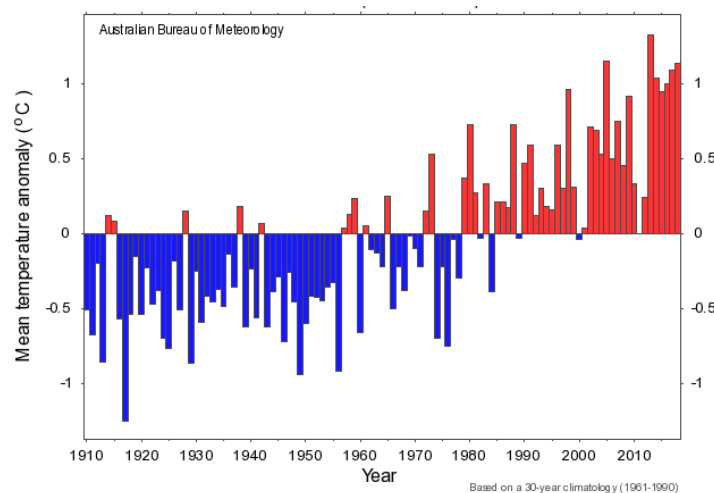


Figure 5-4. Mean temperature anomaly (°C) in Australia from 1910 to 2018 (BOM 2018).

Many species are further threatened by a lack of recognition of the severity of climate change by politicians (Woinarski *et al.* 2017). The speed of recent climate change is unprecedented, and many species are not able to adapt to such rapid alterations to their ecological niches. Some small arid zone Australian mammals, including *S. psammophila*, may have been able to survive the most recent wave of mammal extinctions by exploiting dense habitats and subterranean shelters (Chapter 2 and Chapter 3) that provide natural protection against predators and extreme climates (Churchill 2001a, Pavey *et al.* 2017). However, the dense, semi-arid natural refugial habitats preferred by many desert specialists such as *S. psammophila* rely upon favourable climatic conditions (compared with the interior of the arid zone), including lower temperatures and rainfall related ENSO and IOD effects that influence the geographic location of the intermittent rainfall band in southern Australia (Chapter 1). Hence, future climate change is very concerning for *S. psammophila* and many other threatened arid zone species that are considered rainfall-dependent or are semi-arid species distributed in the southern extremities of the Australian arid zone.

5.4.2. Environmental variables and *S. psammophila* ecology

Mean annual temperature and surface geology were the most informative predictors of *S. psammophila* presence and precipitation in the wettest month was also an important predictive variable for the past, present and future distributions of *S. psammophila*.

Temperature and geology commonly limit species' ranges globally and, in Australia, strong rainfall and temperature gradients exist, with precipitation generally decreasing west to east and temperatures generally decreasing north to south (Stewart *et al.* 2018, BOM 2018). The model confirms that the current distribution of *S. psammophila* is constrained by southern, spinifex sand dune and plain habitats found within yellow to orange sandy soils and a semi-arid climate that is influenced by winter rainfall (Fig. 5-3). During the very windy conditions of the mid-Pleistocene, finer yellow to orange sand particles were deposited at higher elevations than heavier dark orange to red sand

particles, causing heterogenous soil landscapes in the arid zone (Madigan 1936, Sheard *et al.* 2006). These lighter yellow to orange sandy soils are preferred by *S. psammophila*, hence, surface geology soils (usually yellow to orange sand dune and sand plain formations) are often an informative indicator of *S. psammophila* presence. Conditions remained windy in Australia between ~20-100 ka BP, thereafter, the winds calmed, and Australia's surface geology became relatively stable. Therefore, the 'Geology' variable used for the SDMs was also suitable for the past models of the MH distribution (approximately 6 ka BP) of *S. psammophila* and for both future timescales of 2050 and 2070 as Australia's surface geology is not likely to change considerably within the next 30-50 years. The IBRA variable used in Chapter 4 was not used for climate change projections as the IBRA boundaries will likely change over time (due to the changing climate which is a component of IBRA bioregional mapping) and are only suitable for present day SDMs. In the climate change models, the important environmental variables, maxSSS threshold and response curve outputs varied from those used in Chapter 4 due to the use of updated occurrence records, lack of the IBRA bioregion variable and the differing MaxEnt features used for the most parsimonious models with the lowest AICc scores. The models in this chapter demonstrate that mean annual temperature, winter rainfall and geology are important determinants of the distribution of *S. psammophila*.

5.4.3. The mid-Holocene past model and recent contractions

The mid-Holocene (MH) SDM is supported by the haplotype network of *S. psammophila* presented by McLean *et al.* (2018), i.e., the model predicts that the WAGVD and YRR populations were connected throughout the GVD, thus, the WAGVD and YRR populations share an ancestral haplotype. Further, the MH model is indicative of the original distribution of *S. psammophila* at the time immediately before the European settlement of Australia as the MH model agrees with the locations of historical records (~50-500 years BP) near Uluru, Yalgoo and Lake Barlee (Chapter 1

and Chapter 4) that were not used for modelling. Hence, between ~50-500 years BP, it appears that the distribution of *S. psammophila* rapidly contracted by 70 % in area from a distribution resembling the MH model to the P model.

As the modelling used bioclimatic and geographical data only (and does not consider factors such as invasive mesopredators, extreme events and habitat loss), climate change has been a major contributing factor affecting the historical range contraction of *S. psammophila*. As many arid zone mammal species disappeared from the south first and then the north (tracking the displacement of the First Australians), the significant benefits of the indigenous management of the arid zone are clearly demonstrated (Finlayson 1936, 1958, 1961, Burbidge *et al.* 1988). For example, the First Australians controlled wildfires, provided dense, long unburned habitats, increased primary resources, protected old growth trees and tree hollows, managed water resources such as Gnamma holes, and thus, maintained a natural balance for the past 60+ ka (Chapter 1). In addition, prior to Europeans, there were no eutherian mesopredators. While climatic conditions became hotter and drier from the mid-Miocene, this was very gradual, and synergistic extinction pressures were not present (Doherty 2015b). However, in a very short window of time, the First Australians were removed, wildfires raged, and feral mesopredators were suddenly widespread, and many arid zone mammal species were not able to endure these extinction pressures. *Sminthopsis psammophila* did not follow the south to north extinction pattern, implying some behavioural adaptation to these pressures. For example, the high mobility of *S. psammophila* together with its preference for long unburned dense habitats and use of concealed burrows (Chapter 2 and Chapter 3) may have allowed the species to persist alongside feral mesopredators while other species without these adaptations perished. However, when Australia's climate rapidly began to change due to the industrial revolution (over 1 °C of warming during the past 100 years), this additional and significant pressure for *S. psammophila*, and many other arid zone species, may have

caused distributional contractions towards denser habitats with more favourable climates (wetter and cooler) within southern and eastern regions (Law *et al.* 2017).

5.4.4. Important pressures that may affect the future distribution of *S. psammophila*

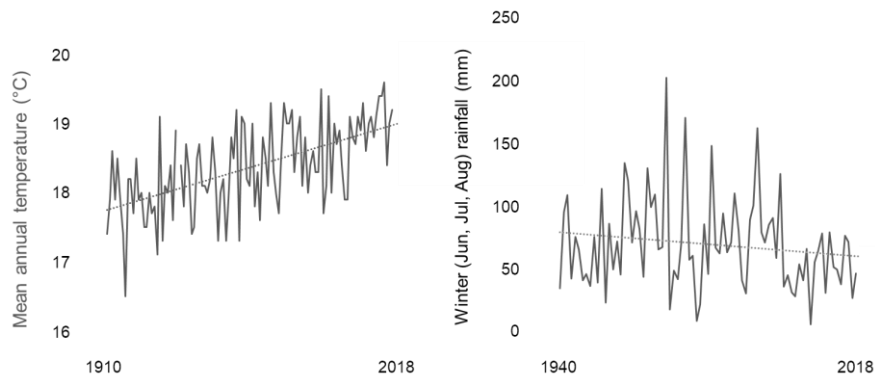


Figure 5-5. Historical climate data from the nearest long-term monitoring weather station (Kalgoorlie-Boulder) to the study site indicates the changing climate of the arid zone (BOM 2018). Left: mean annual temperature (°C) and right: winter rainfall (mm).

The future SDMs demonstrate that the distribution of *S. psammophila* is predicted to continue to contract southwards and eastwards as it tracks further changes to Australia's temperature and rainfall. Historical arid zone climatic records are given in Fig. 5-5. The SDMs predicted that, by 2050, almost all WAGVD habitat will become climatically unsuitable for *S. psammophila* under the “business as usual” (RCP 8.5) emissions scenario, i.e., if there is no action on greenhouse gas emissions and global warming continues at the current rate. In the 2070 (RCP 8.5) emissions scenario, both the WAGVD and YRR populations are predicted to become climatically unsuitable and the geographic distribution of *S. psammophila* may contract in area by up to 80 % throughout Australia. As *S. psammophila* is geographically restricted at its southern extent due to the cessation of appropriate soil types and *Triodia* spp. habitats, and is climatically pressured at its northern extent, the habitable zone for *S. psammophila* will significantly decrease in the future. *Sminthopsis psammophila* is therefore at considerable risk of extinction due to climate change.

5.4.5. Limitations

The increasing frequency and severity of extreme events, such as droughts and wildfires, is known to cause sudden population crashes (e.g. Welbergen *et al.* 2007). The future occurrence of these events may be very difficult to predict and are not factored into the models. Hence, the future predictions in Chapter 5 may be conservative estimates. The future predictions of the models are only as accurate as the GCMs used, and GCMs can be affected by many factors, such as an imperfect mathematical equations, the power of computers, an inability to reproduce vital atmospheric phenomena, and inaccurate depictions of complex natural phenomena (Legates 2002). The known occurrence data for *S. psammophila* remain sparse, hence, the accuracy of future models may be further improved with new occurrence records. Thus, it is recommended that the modelling procedure be repeated when new data or methods are available.

5.4.6. Conservation management

Sminthopsis psammophila is predicted to be severely threatened by future climate change. Populations further north (WAGVD and YRR) are at a higher climatic risk than the southern EP population (Fig. 5-1 and 5-2). However, the EP population itself, although a climatic refuge, is also at risk of contraction. Therefore, it is important to monitor all populations to compare how the distributional contractions predicted by the SDMs track against real range contractions. A range of southern natural refugial habitats and reserves within EP, QVS and the southern YRR should be managed to prioritise the protection of long unburned, dense habitats that are required for *S. psammophila* and sympatric arid zone species. Conservation planners should consider the future climates of planned fenced exclosures as northern and western habitats are predicted to become increasingly unsuitable for *S. psammophila* and sympatric desert species over the next 50 years. Regions of the far southwest of Western Australia (outside of the arid zone) were indicated as climatic refuges by the modelling (Fig. 5-1

and Fig. 5-2). Translocations to constructed artificial fenced reserves with transplanted soils, seeds and vegetation from natural arid zone habitats may be required. As future SDMs indicate climatically and geographically suitable habitat only, SDMs must be considered with accurate fire mapping and/or fire aging methods for informed conservation management decisions. In addition, respecting and acknowledging that the First Australians have 60+ ka of knowledge regarding the changing climate (Green *et al.* 2010) is an essential part of threatened species management in Australia. Empowering Indigenous-led management and practice is vital to improve threatened species conservation globally (Mullins *et al.* 2020). The EPBC Act (1999) is currently being amended (www.epbcactreview.environment.gov.au). An effective conservation management suggestion arising from this chapter is to lobby the government with evidence-based research regarding the impacts of climate change. Without the intervention of conservation planners, the biodiversity and climate crisis will continue to cause further extinctions in Australia (Woinarski *et al.* 2017).

The population estimation methods and assumptions proposed in Chapter 4 were used to calculate the total population declines between the present and future scenarios for *S. psammophila* in (a) the WAGVD and (b) Australia (Table 5-3). The drought-affected population of *S. psammophila* in the WAGVD was 10 % of the healthy (non-drought) population as a mean of 10 individuals were captured in the study site during non-drought periods (2015-2018), whereas one individual was captured during the drought in 2019 (Chapter 4). Hence, even under an optimistic future emissions scenario (RCP 4.5) in drought-affected periods *S. psammophila* throughout Australia may meet the IUCN 'Endangered' criteria by 2050 and the 'Critically Endangered' criteria by 2070 (IUCN 2018). There are large disparities when predicting total population declines for just the WAGVD population and *S. psammophila* throughout Australia (Fig. 5-2 and Table 5-3). In the WAGVD, *S. psammophila* is at an increased risk of rapid population decline due to climate change, even under an optimistic future scenario (RCP 4.5), compared with at a national level. Hence, this again supports that the WAGVD

population should be managed separately from the remainder of the continental population.

Table 5-3. Area of preferred habitat and total population decline estimate from present under a range of future climate change scenarios. RCP = representative concentration pathway; ka BP = thousand years before present; WAGVD = Western Australian Great Victoria Desert. Area a) = climatically and geographically suitable predicted habitat. Area b) = climatically and geographically suitable and long unburned (20+ years since fire) habitat.

Model	Year	RCP	Area a) (km ²)	Area b) (km ²)	Area of preferred habitat (km ²)	Number of individuals #	Total population difference
WAGVD							
Past	6 ka BP	-	118,432	▲			
Present	2020	-	28,048	2,805	1,206	1,723	-
Future	2050	4.5	12,384	1,238	533	761	-962
Future	2050	8.5	1,296	130	56	80	-1,643
Future	2070	4.5	576	58	25	35	-1,688
Future	2070	8.5	0	0	0	0	-1,723
Australia							
Past	6 ka BP	-	327,424	▲			
Present	2020	-	98,096	9,810	4,218	6,026	-
Future	2050	4.5	97,568	9,757	4,195	5,993	-33
Future	2050	8.5	72,864	7,286	3,133	4,476	-1,550
Future	2070	4.5	36,832	3,683	1,584	2,263	-3,763
Future	2070	8.5	19,200	1,920	826	1,179	-4,847

▲ It was not possible to estimate long unburned habitat for past scenarios. # Estimated number of individuals in non-drought periods and if home ranges do not overlap (see Chapter 4). Drought-affected number of individuals = 10 % of the number of individuals during non-drought periods.

5.4.7. Summary

This chapter demonstrates that SDMs are useful conservation management tools to identify populations that are vulnerable to anthropogenic climate change. Estimations were made to determine the area of preferred habitat and the number of individuals for

S. psammophila. Projections of past and future distributions were made for a rare and threatened arid zone species with sparse occurrence data. Again, the use of geographical GIS layers improved SDM predictions, hence, it is suggested that (if relevant to the species being modelled) these layers are included with bioclimatic layers for a robust modelling approach. While the results of this chapter raise concerns for the conservation of *S. psammophila* and potentially for many other species, an optimistic attitude toward conservation and climate change is required to give us a choice to act (Balmford 2012, Garnett *et al.* 2018a, Figueres and Rivett-Carnac 2020). There has already been significant reduction of fossil fuels, technological innovation, and effort to curb climate change by many world leaders, organisations, industries, and countries. Maintaining an optimistic belief that we can tackle this existential crisis requires perseverance, behavioural change, and inspiration (Figueres and Rivett-Carnac 2020):

“The period between now and 2030 is going to have more of an impact on the future of the Earth than any other decade in history, and while that can seem daunting, we truly have everything we need to solve this crisis. We can get on track and history will look back at 2020 as humanity’s best hour.”

The estimations made for the area of preferred habitat for *S. psammophila* are perhaps more useful than estimations of the number of individuals, especially for rare and threatened arid zone species, as population density estimates are very difficult to determine for fluctuating populations with potentially overlapping ranges (Chapter 3) that are affected by many immeasurable factors (Churchill 2001a, Ward *et al.* 2008, Woinarski and Burbidge 2016). However, with robust SDMs and an ecological understanding of the species, it is possible to estimate the extent of occurrence (area of preferred habitat) of such species, which may be helpful for conservation status assessments.

Chapter 6: General Discussion



6.1. Overview

This chapter considers the conclusions from all previous chapters to address the key knowledge gaps and central research questions for *S. psammophila*, an 'Endangered' (EPBC 1999), semi-arid desert dwelling small mammal. Results are reviewed regarding the aims and hypotheses of this study and are contextualised with previously published literature. The findings are discussed against a more general background of ecological principles and conflicting or unexpected findings are considered. The principal implications and the significance of the study are given regarding the conservation management of a) *S. psammophila*, b) Australian desert ecosystems and c) threatened arid zone species globally. The chapter concludes with limitations to the study, possible future applications of the research and closing remarks.

6.2. Habitat preferences and small desert mammals

A comprehensive autecological and radio tracking approach confirmed the hypothesis that *S. psammophila* preferred sheltering in burrows located within long unburned, dense lower stratum habitats. Previously, the sheltering preferences of the Western Australian Great Victoria Desert (WAGVD) *S. psammophila* population were unknown and proxy sheltering preferences of the Eyre Peninsula (EP) population were typically applied during targeted surveys. However, this may have caused historical detection difficulties due to regional differences in sheltering habitat preferences. Habitat preferences appear to be specific to each population, however, both the WAGVD and Yellabinnia Regional Reserve (YRR) populations of *S. psammophila* commonly shelter within burrows underneath mature *Triodia* spp. hummocks. Conversely, 'Stage 3' spinifex hummock shelters in younger fire age habitats may be preferred in the EP population (Churchill 2001a). This agrees with the premise that site-specific habitat preference studies are required for small desert mammal populations that are widely

separated and/or have no historical geographic connectivity (Driscoll *et al.* 2010, Moore *et al.* 2015, McLean *et al.* 2019).

Burrowing and the use of long unburned dense habitats likely facilitate the survival of *S. psammophila* within a landscape extensively modified by Europeans, allowing it to persist where many sympatric small mammal species have been recently extirpated. Thus, maintaining, restoring, protecting, and connecting the preferred habitats of *S. psammophila*, i.e., long unburned spinifex swales, sand plains and dune slopes in the WAGVD, is a key conservation priority. Logistically, the preservation of remote and flammable arid zone habitats such as those used by *S. psammophila* is most easily achieved by preventing large-scale catastrophic wildfires (Bowman *et al.* 2020).

Changes in wildfire patterns have strongly affected habitat use by sympatric arid zone species within Earth's deserts (Brooks 1999, Bradstock *et al.* 2002, Driscoll *et al.* 2010, Gray and Dickson 2015). The findings of Chapters 2 and 3 support that wildfire management is a very high priority for the conservation of arid zone biodiversity.

Globally, the methods that are most effective in wildfire management integrate modern methods (e.g. aerial burns) with cultural or indigenous burning which has been used for many thousands of years worldwide and is particularly important for the conservation management of arid zone ecosystems to maintain an ecological balance (Burbidge *et al.* 1988, Bowman 1995, Rose 1997, Bayly 1999, Moorcroft *et al.* 2012, Pascoe 2014, Bowman *et al.* 2020).

Burrows, logs, and *Lepidobolus deserti* hummock shelters were repeatedly used as diurnal shelters by *S. psammophila* and had beneficial thermal properties (Chapter 2). Burrowing is rarely reported for *Sminthopsis* spp. and few dunnart species are reported to excavate their own burrows (Morton 1978, Dickman *et al.* 1993, Haythornthwaite and Dickman 2006, Waudby and Petit 2017, Woolley 2017, Baker and Dickman 2018, Bleicher and Dickman 2020). However, the conclusions of Chapter 2 disagree with this premise and confirm that burrowing is important for *S. psammophila* and may have

been previously overlooked for sympatric arid zone species. Globally, many small arid zone mammal species conserve energy and water by entering torpor and/or using shelters such as burrows that reduce energetic costs within the extreme climates of their desert environments (McNab and Morrison 1963, Downs and Perrin 1990, Geiser and Ruf 1995, Kinlaw 1999, Scott 2000, van Dyck and Strahan 2008, Schwimmer and Haim 2009, Degen 2012, Baker and Dickman 2018). Therefore, the sheltering behaviour of *S. psammophila* agrees with our current understanding of small desert mammal survival. While preferring burrows, *S. psammophila* also used atypical shelter types (Fig. 6-1).



Figure 6-1. Burned sheltering habitat (a hollow within a burned mallee, *Eucalyptus* sp. stump; indicated by arrow) was used once only ($n = 211$ shelters located in total).

Behavioural flexibility is one way of increasing energy returns in an environment that has unpredictable resources (Scott 2000). Small desert mammals do not often use burned habitats, often preferring dense habitats that reduce predation risk and yield increased primary resources (Reichman and Smith 1990, Dickman *et al.* 1993, Brown *et al.* 1999, Laundré *et al.* 2001, Fisher and Dickman 1993, Bos *et al.* 2002, Bleicher and Dickman 2020). Thus, the use of burned habitat by *S. psammophila* - although very rare - is a notable adaptation. Such flexibility in habitat use may allow *S. psammophila* to persist in worsening wildfire conditions (Price and Rind 1994, IPCC 2014, Dutta *et al.* 2016, CSIRO 2017). Its large home ranges, high mobility and use of evasive anti-predation techniques (Chapter 3) may allow recolonisations across burned habitats and into adjacent long unburned habitats. Thus, this behavioural flexibility is a

hopeful sign that some small desert mammals can adapt to the destructive impact of wildfires. Despite its common name of the sandhill dunnart, *S. psammophila* did not prefer “sandhill” habitats. Similarly, ‘Woodland’, ‘Mulga’ and ‘Burned’ habitats were avoided. These habitat types have inappropriate soil substrates for *S. psammophila* burrowing and/or lack a dense lower habitat stratum of spinifex to reduce predation risk (Chapter 3). Therefore, the availability of suitable refuge habitats and soils for burrowing are important in determining the presence of *S. psammophila*.

The specific habitat requirements of *S. psammophila* make it an excellent indicator species for dense, ‘healthy’ natural refugial habitats (Landres *et al.* 1988, Caro 2010). The prevention of wildfires is a key component of the conservation of *S. psammophila* and will protect many species within its geographical range, making it a valuable regional umbrella species (Meffe and Carroll 1997, Simberloff 1998, Barua 2011). In addition, *S. psammophila* is an ‘Endangered’ (EPBC 1999), attractive, and ecologically intriguing animal that provokes a strong emotional response. Therefore, it is also an effective flagship species that can improve the conservation management of the Great Victoria Desert (Meffe and Carroll 1997, Ducarme *et al.* 2013, GVDBT 2017).

Overall, the findings highlighted that tracking many individuals over long periods of time (four years in this study) is helpful to elucidate a species’ full range of behaviour, and that it is important to correctly quantify the site-specific habitat preferences of threatened and/or rare species as these can differ across populations.

6.3. Foraging behaviour, ranging and diet

The ranging behaviour and foraging preferences of *S. psammophila* in the WAGVD were reported in Chapter 3. Novel tracking methods used GPS data loggers and preferred habitat use analyses which provided unique insights into the nocturnal ecology of a rare and threatened small desert mammal. As in Chapter 2, *S.*

psammophila preferred dense foraging habitats, particularly dune slopes, which likely yielded higher invertebrate resources and reduced predation risk. This agrees with the premise that many species use optimal foraging strategies to increase resource intake and minimise predation risk by selecting certain habitat classes (Cowie 1977, Brown 1988, Cowlshaw 1997, Kotler *et al.* 1993, Brown *et al.* 1994, Bleicher and Dickman 2020). Desert mammal species are at risk of predation by both native and introduced predators (Burbidge and McKenzie 1989, Baker and Dickman 2018, Woolley *et al.* 2019). Predation risk typically increases during moonlit nights because of the beneficial effect moonlight has on the nocturnal vision of many predators (Williams *et al.* 1993, Olsen 2011). However, periods of high luminosity had no statistical effect on the foraging behaviour of *S. psammophila*. Therefore, *S. psammophila* probably uses similar evasive techniques to sympatric small desert mammals such as quick escapes or the use of spinifex hummocks as temporary refuges to mitigate predation risk (e.g., Randall 1993). Evasive behaviour is not always a successful method; this may be because native Australian species are less familiar with introduced predators (Short *et al.* 2002, Salo *et al.* 2007). One tracked *S. psammophila* individual was killed but not eaten by a feral cat during the study (Fig. 6-2).



Figure 6-2. Surplus killing of a radio tracked *S. psammophila* by a feral cat, *Felis catus*. The teeth and jaws of a feral cat museum specimen were matched to bite marks on the individual. Conversely, many small mammals reduce predation risk by limiting foraging during periods of high luminosity (e.g., Kaufman and Kaufman 1982, Clarke 1983). As only one individual out of 40 tracked individuals was known to be killed by a feral cat and *S.*

psammophila appears to persist in their presence (Chapter 3), feral cats are a threat to the species but not as significant a threat as wildfires and the associated habitat destruction. However, *S. psammophila* is listed within the top five species that are most likely to be killed by feral cats due to their traits (Wooley *et al.* 2019). Hence, the conservation of *S. psammophila* and many sympatric species will likely benefit from culling feral mesopredators within preferred habitats or known areas of high occupancy (Denny and Dickman 2010, Doherty *et al.* 2015a). The control of feral predators is a pressing issue for many species worldwide. An emerging discussion is the use gene editing technologies such as CRISPR-Cas9 or “prime-editing” to eradicate feral mesopredators (Moro *et al.* 2018, Anzalone *et al.* 2019). In the Australian arid zone in particular, it may be helpful to cease dingo culling or dingo control methods to suppress feral cat and red fox populations (Johnson *et al.* 2007, Letnic and Dickman 2012, Smith 2015). Such methods will reduce predation pressure for small mammals.

The mean home range of *S. psammophila* (70 ha) was much larger than previously reported and the maximum home range was 274 ha. Therefore, the conclusions of Chapter 3 agree with the premise that Australian arid zone mammals often have large home ranges and/or a high mobility to track shifting areas of resources within their unpredictable environments (Dickman *et al.* 1995, Schlesinger and Pilmanis 1998, Letnic 2001, Bos *et al.* 2002, Haythornthwaite and Dickman 2006, Dickman *et al.* 2011). There was a strong effect of sex on ranging behaviour, which agrees with the hypothesis in Chapter 3 and previous research on sympatric small desert mammals (McLean 2015, Friend *et al.* 1997, Baker and Dickman 2018). Wide male ranging indicates that *S. psammophila* probably uses a polygynous or polygynandrous mating strategy, with males travelling over the ranges of several potential female mates (Bedford *et al.* 1984, Rose *et al.* 1997). The results support that idea that the conservation management of *S. psammophila* and sympatric small desert mammals requires the protection of large, contiguous areas of natural refugial habitats with a

dense lower stratum to maintain normal foraging and mating behaviour. Again, the most effective way of achieving this is through wildfire management.

Overall, the findings support the premise that small desert mammals have specialised foraging and dietary preferences to enable their survival in arid environments (Perrin and Swanepoel 1987, Letnic. 2001, Brown and Ernest 2002, Yarnell *et al.* 2007, Degen 2012, Baker and Dickman 2018). Localised resource islands or patches with a high diversity and density of shrubs were important for *S. psammophila*, supporting that foraging patch use is important for sympatric species globally (e.g., Brown 1988, Bowers and Dooley 1993, Ziv and Kotler 2003). The niche partitioning theory refers to the process by which natural selection drives competing species into different niches of resource use (MacArthur 1958). For *S. psammophila* and two competing *Sminthopsis* spp. this was neither proved or disproved as there was a high degree of dietary overlap for *S. psammophila* and *S. hirtipes*, however, *S. dolichura* appeared to prefer a wider range of larger prey. This may be explained by the geographic range of each dunnart species; *S. psammophila* and *S. hirtipes* are arid zone species while *S. dolichura* is also found in more mesic habitats (Menkhorst and Knight 2001). Ants were an important dietary resource for *S. psammophila* and *S. hirtipes*, suggesting facultative dietary specialism (Shipley *et al.* 2009). This is an intriguing discovery as ants were not thought to be commonly consumed by small desert mammals due to costs associated with their digestion (Greenslade 1984, Fisher and Dickman 1993). However, many desert mammals are often forced to consume poor quality resources to facilitate their survival during resource-limited conditions and subsequently use energy saving strategies, e.g. torpor, to decrease digestion costs (Degen 2012). Hence, an interesting area to explore is the importance of ants or other ubiquitous but not easily digested invertebrate prey species, e.g., termites, as a staple resource for carnivorous desert dwelling species globally.

6.4. Species distribution models, climate change and conservation status assessments

Species distribution models (SDMs) are helpful to inform the conservation management of rare and/threatened species and to assess their vulnerability to climate change (Peterson and Vieglais 2001, Beaumont and Hughes 2002, Peterson *et al.* 2002, Bakkenes *et al.* 2002, Williams *et al.* 2003, Thomas *et al.* 2004, Thuiller *et al.* 2006, Guissan *et al.* 2013). Future climate change will likely change conservation priorities, and conservation planners must identify areas that will provide suitable refugial habitats for species in a changing climate (e.g., Adams-Hosking *et al.* 2011). Chapters 4 and 5 used SDMs to provide new information on the past, present and future distributions of *S. psammophila*. Environmental variables that predicted the species' presence used both geographical (surface geology and IBRA bioregion) and climatic data, which improved model predictions. Therefore, sympatric arid zone species (that are restricted to specific soil types) may benefit from modelling with similar geological GIS data sets. During ground-validation of the SDMs, *S. psammophila* was confirmed in 18 new locations and a novel population 150 km north of the species' range was detected (Chapter 4). Therefore, SDMs are helpful to confirm new occurrence records and delineate range boundaries for rare desert mammals.

As hypothesised, *S. psammophila* is probably restricted to within or near its known southern semi-arid desert range. During the study, mesic species such as the western pygmy possum, *Cercartetus concinnus*, and the Western Australian carpet python, *Morelia spilota imbricata*, were recorded in the range of *S. psammophila*, indicating that an important biological interzone may exist between the central deserts and wetter mesic habitats. The southern semi-arid interzone supports some of the richest known ant faunas in Australia (Greenslade and Greenslade 1989) - thus, this may explain the large proportion of ants in the diet of *S. psammophila* (Appendix C). The results of the past SDMs (Chapter 5) propose that the original pre-European distribution of *S.*

psammophila was much more widespread but likely rapidly contracted due to climate change within the past ~50-500 years. Conversely, many Australian arid zone mammals are thought to have contracted because of land use changes and the impacts of feral mesopredators (Finlayson 1936, 1958, 1961, Burbidge *et al.* 1988). Phylogeographic evidence indicates that the historical ranges of multiple arid-adapted dasyurid species contracted and expanded because of Pleistocene climate change (Umbrello *et al.* 2020). Hence, the findings of Chapter 5 support that anthropogenic climate change may be a significant cause of many recent arid zone mammal range contractions.

The future SDMs (Chapter 5) report that rapid anthropogenic climate change poses a significant risk to *S. psammophila*, as it does to many species within the deserts of the southern hemisphere (Williams 2014). Fossil fuel use, changes in land use and industrialised agriculture have caused the existential boundaries of three vital terrestrial systems (biodiversity loss, climate change and the nitrogen cycle) to be exceeded (Dirzo *et al.* 2012, Rockström *et al.* 2016). The geographical ranges of numerous Australian species have recently contracted southwards and eastwards, tracking areas with favourable and denser habitats, cooler temperatures, and higher rainfall (Dexter *et al.* 1995, Hughes 2003, Adams-Hosking *et al.* 2011, IPCC 2014, Law *et al.* 2017). Similarly, *S. psammophila* is predicted to contract southwards and eastwards and two strongholds (the WAGVD and YRR populations) may become climatically and geographically unsuitable for the species by 2050-2070. However, the forecasted range contraction of *S. psammophila* could be halved if there is global action on anthropogenic climate change. Therefore, the conclusions of this research agree that reducing greenhouse gas emissions and employing technologies to reduce the impacts of climate change are essential conservation management priorities for *S. psammophila* and many species worldwide (Steffen 2009, IPCC 2014, CSIRO 2017). Overall, SDMs were proven to be very helpful conservation management tools that can

determine a species range, discover new populations, and assess which species are most vulnerable to climate change.

There is a large effect of spatial scale on the conservation status assessments of many highly fragmented arid zone species such as *S. psammophila* (Chapter 5). Problems of spatial scale can influence the outcome of IUCN Red List assessments and could be a source of inconsistency and bias (IUCN 2019). It is impossible to provide any strict but general rules for mapping taxa or habitats; the most appropriate scale will depend on the taxon in question, and the origin and comprehensiveness of the distribution data (IUCN 2019). Hence, for rare, patchily distributed species such as *S. psammophila*, the effect of spatial scale must be considered. The results of Chapter 5 indicate that the population of *S. psammophila* in the WAGVD is facing a higher risk of local extinction, hence, the findings agree that each population requires management as a distinct unit (Crandall *et al.* 2000, Lindenmayer *et al.* 2010, McLean *et al.* 2018) rather than on the continental scale of Australia. Sympatric arid zone species that may have similar issues with spatial scale and conservation status assessments are probably rare with patchy, widely separated distributions that are prone to destruction by annual wildfires. Species that are better studied and distributed within a single region may fare better with traditional area of extent or area of occupancy estimates.

However, even when assessed at a continental scale, *S. psammophila* likely already possesses a low population size and is restricted to precarious, flammable, long unburned habitats that are decreasing annually due to increasingly frequent, unmanaged, and severe wildfires (Woinarski and Burbidge 2016). For an 'Endangered' IUCN assessment, a threatened species must meet only one 'Endangered' criteria [A to E]. The best available evidence (including model projections) must be used to consider if a species is at an extremely high risk of extinction in the wild (IUCN 2019). As the number of mature individuals is difficult to determine for *S. psammophila* and most dynamic, boom-bust desert dwelling species (Chapter 4), calculating the "area of

preferred habitat” (Table 5-3) with SDMs and the assumptions in Chapter 4 is more useful for conservation status assessments of fragmented arid zone species. The “area of preferred habitat” or the IUCN “extent of occurrence” area for *S. psammophila* throughout Australia was estimated as 4,218 km². Therefore, this fulfils the IUCN (2019) ‘Endangered’ criteria [B1ab(i-v)c(i-iv)] wherein the extent of occurrence is estimated to be less than 5,000 km². *Sminthopsis psammophila* is (a) severely fragmented or known to exist at no more than five locations (EP, YRR and WAGVD) and there is (b) a continuing decline, observed, inferred or projected, or (c) extreme fluctuation in any of the following: extent of occurrence, area of occupancy, area, extent and/or quality of habitat, number of locations or subpopulations, number of mature individuals (IUCN 2019). Therefore, the conclusions of Chapter 5 demonstrate that *S. psammophila* mistakenly reclassified by the IUCN Red List to ‘Vulnerable’ (Woinarski and Burbidge 2016) and should be classified as ‘Endangered’ by the IUCN. Using the same assessment method, the population of *S. psammophila* in the WAGVD may be ‘Critically Endangered’ [B1ab(i-v)c(i-iv)] by 2050 (RCP 8.5), again highlighting that this population is more vulnerable to future climate change (Table 5-3).

6.5. Limitations

As the GVD and central arid zone areas in general of Australia are very remote and often difficult to access, there are limited ecological studies, particularly for small, nocturnal, and rare species such as *S. psammophila*. Hence, one of the limitations to the scope of the study was the paucity of background information. This study has provided robust data on the WAGVD population, which are supported by data from the YRR population (Churchill 2001a, 2001b). However, it is recommended that the EP population be studied further with GPS data loggers to better determine the species’ habitat preferences and sheltering behaviour.

During the study, fire age estimates were limited by the age of available satellite imagery (40 years in the WAGVD). This can be improved (see Section 6.6). The SDMs used in Chapters 4 and 5 did not model the effects of extreme events (Fig. 6-3). However, extreme events can cause mass die-offs (e.g., Welbergen *et al.* 2007) and have been used to predict future outcomes for threatened species globally (e.g., Rasztoivits *et al.* 2014). Hence, *S. psammophila* and sympatric arid zone species may be at a higher risk of extinction than proposed by this thesis, and further modelling of extreme drought and wildfire events may be required.



Figure 6-3. Large wildfires (left), droughts and hot winds (right) destroyed sensitive Western Australian Great Victoria Desert (WAGVD) habitat in 2019.

Radio tracking can be challenging within the remote habitats of *S. psammophila*. For example, two wide ranging reproductively active male *S. psammophila* were not able to be located and their data were never recovered (Chapter 3). Therefore, methods that enable the recovery of GPS data loggers, e.g., radio tracking drones, should be used to improve outcomes.

Funding was limited as the project was self-funded, however, there were three major financial contributors (the GEMG, APA and Kingfisher Environmental) with significant in-kind support from TGM. The study was possible as it was “piggy backed” with existing surveys for the aforementioned parties, hence, the timing of the research was limited by the logistical restraints of the stakeholders. Field work was also limited by environmental conditions, i.e., it was not safe to perform remote field work in the GVD during periods of increased wildfire risk (summer) or flooding risk (winter).

While ants were extremely common within the faecal pellets of *S. psammophila*, the morphological frequency of occurrence analyses used in Chapter 3 are not the most accurate method to determine a species' diet. Future dietary studies are recommended to use either a molecular or percentage by weight/volume method as these methods have been successfully used for insectivorous mammals (Abensperg-Traun and Steven 1997, Zeale *et al.* 2011).

6.6. Future applications and suggestions for arid zone management

This research primarily addresses the conservation management of *S. psammophila*, however, the methods used can improve the conservation management of threatened arid zone species globally. Sections 6.2 to 6.4 highlighted three key conservation management improvements for arid zone species. Priorities are to a) correctly determine the specific habitat preferences of each population of highly fragmented and/or rare arid zone species, b) prevent catastrophic wildfires and c) reduce the impacts of anthropogenic climate change. Secondary issues of feral mesopredator control and classifying the correct conservation status of species were also highlighted.

Identifying and managing a species' preferred habitat is essential for its successful conservation. Habitat preferences analyses were improved for *S. psammophila* by using improved radio tracking methods and innovative GPS data loggers. Habitat preference analyses were improved using *phuassess* (Fattorini *et al.* 2017) and by tracking a large number of individuals. Therefore, it is recommended that future studies of small desert mammals globally may benefit from using a similar approach. There are numerous management options available to protect the preferred habitats of arid zone species. For example, artificial lower stratum habitats could be deployed within burned and/or open areas that connect preferred habitats, thus, increasing invertebrate

biodiversity and lowering predation risk (Webb and Shine 2000, Crooks and Sanjayan 2006, Threlfall *et al.* 2017). Arid zone habitats may benefit from the distribution of artificial food and water during droughts (e.g., Arid Recovery Reserve 2019). The effects of artificial resource supplementation should be assessed by measuring, for example, vegetation growth rate, habitat density or the number of mature individuals.

For effective wildfire management, it is essential develop relationships with indigenous stakeholders, ecologists, land managers and environmental leaders by applying traditional wildfire management methods and knowledge to facilitate better informed, reciprocal conservation and cultural management programs (Burbidge *et al.* 1988, Bowman 1995, Rose 1997, Bayly 1999, Pascoe 2014, Bowman *et al.* 2020). A key indigenous method of wildfire management used globally is small-scale patch burning which maintains heterogenous habitat mosaics (Gould 1971, Minnich 1983, Hallam 1985, Haydon *et al.* 2000, Burrows *et al.* 2006, Smit *et al.* 2013). Heterogenous habitat mosaics have differing structural densities, vegetation richness or seral stages, and are critical for native mammal species richness (Kerr and Packer 1997, Letnic 2001, Holland *et al.* 2007, Bird *et al.* 2008) as invasive species such as the house mouse and the feral cat prefer disturbed vegetation (Holland *et al.* 2007, McGregor *et al.* 2015, 2017). Therefore, the protection and restoration of heterogenous mosaics in deserts may protect *S. psammophila* and sympatric species.



Figure 6-4. Poor management of Queen Victoria Spring Nature Reserve (QVS) in Australia must be improved for the successful conservation of *S. psammophila* and many semi-arid desert species. Photographs taken before (left, March 2018, photo credit: Joanna Riley) and after (right, May 2019, www.lenbeadell.com.au) a large wildfire.

Legally protected reserves with key habitats or areas that have a high predicted probability of presence for arid species should be managed against large wildfires as a priority (Fig. 6-4). As anthropogenic climate change poses a significant risk for many arid zone species globally, it is recommended that their conservation management uses SDMs to prioritise which species are most vulnerable. Many arid zone populations are affected by seasonal/summer wildfires and the increasingly severe impacts of climate change; thus, many populations require annual monitoring to assess yearly changes to habitat extent, health, and the number of mature individuals. Long-term monitoring may be helpful to compare the predictions of SDMs with real time range contractions, to assess whether species' range contractions track model predictions. Other methods to mitigate the effects of climate change include translocations to protected fenced reserves within climatic refuges. This should only be undertaken when disease transfer risk is minimal; it may be counterproductive to translocate individuals from populations that have no past connectivity. Constructing new fenced exclosures or artificial desert ecosystems in mesic climates with transplanted topsoil, seed, and vegetation may be required for the conservation of arid zone species to reduce the impacts of droughts (Fig. 6-5).

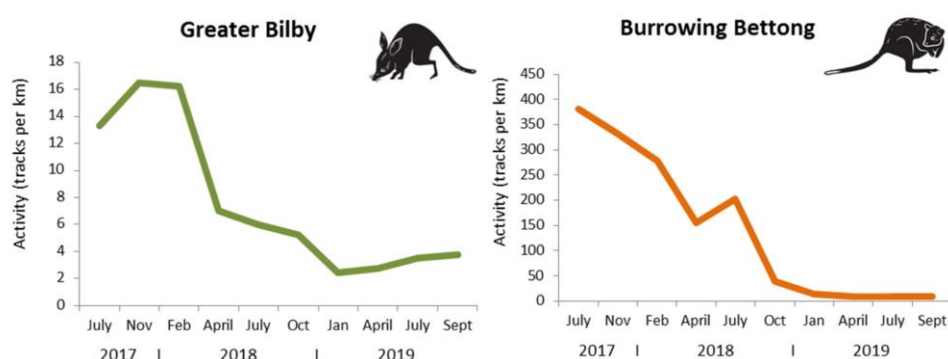


Figure 6-5. Threatened mammal species activity in conservation reserves within the Australian arid zone has rapidly declined due to droughts. Data were extracted from Arid Recovery Reserve (2019), a fenced predator-free reserve where the total rainfall in the past two years was ~90 mm.

6.7. Closing remarks

I hope that the conclusions of my research will ignite interest in the conservation of *S. psammophila*, Australia's threatened species and desert ecosystems globally. While there are significant threats and challenges facing Earth's remaining biodiversity, there is also hope for the future. I pay my respects to the Tjuntjuntjara community and the Anangu tjuta pila nguru people, to all people of the beautiful Western Deserts and indigenous Australians and elders - past, present and emerging. I am confident that we can work together to protect iconic species such as *S. psammophila* and look forward to future developments and collaborations.



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Appendices

Appendix A. Site locations and descriptions for radio and GPS tracked *S. psammophila* in the Western Australian Great Victoria Desert between 2015 and 2019. Habitat classes: 1) 'Swale or sand plain'; 2) 'Crest'; 3) 'North slope'; 4) 'South slope'; 5) 'Woodland'; 6) 'Mulga' or 7) 'Burned' (detailed habitat class descriptions are given in Table 1. WGS 1984 datum. * = site partially burned.

Site	Longitude	Latitude	Available habitat classes	Date of most recent burn at time of tracking	Dominant spinifex <i>Triodia</i> spp.	Dominant shrub species	Mean minimum fire age (years)	Minimum fire age range (years)	<i>S. psammophila</i> ID
7	124.2499	-29.2568	1 – 6	Dec 2001	<i>T. desertorum</i>	<i>Thryptomene biseriata</i> , <i>Aluta maisonneuvei</i> , <i>Acacia spinosissima</i>	30+	12 - 40+	08, 12, 15, 16, 32, 37, 41
9	124.2866	-29.2582	1 – 6	N/A	<i>T. desertorum</i>	<i>A. maisonneuvei</i> , <i>T. Biseriata</i> , <i>A. Spinosissima</i>	40+	40+	05, 26, 40
10	124.3052	-29.2567	1 – 7	N/A * Dec 2016	<i>T. desertorum</i>	<i>A. maisonneuvei</i> , <i>Baeckea</i> sp. GVD, <i>Allocasuarina</i> spp.	39+	40+ 0 - 40+	03, 04, 09 * 21, 22, 30, 43
11	124.0636	-29.5568	1 – 6	Nov 2002	<i>T. desertorum</i>	<i>Bertya dimerostigma</i> , <i>A. Maisonneuvei</i> , <i>Hakea francisiana</i> , <i>Grevillea juncifolia</i>	12.5	10 - 20	01, 10
12	124.0923	-29.2544	1 - 6	N/A	<i>T. desertorum</i> and <i>T. basedowii</i>	<i>Acacia helmsiana</i> , <i>A. maisonneuvei</i> , <i>G. juncifolia</i> , <i>Baeckea</i> sp. GVD	40+	40+	35
13	124.1201	-29.2545	1 – 6	N/A	<i>T. desertorum</i> and <i>T. basedowii</i>	<i>Acacia helmsiana</i> , <i>A. maisonneuvei</i> , <i>G. juncifolia</i> , <i>B. dimerostigma</i>	40+	40+	14, 29, 39
14	124.3823	-29.2507	1, 5, 6	January 2002	<i>T. basedowii</i> and <i>T. sp. rigidissima</i>	<i>A. maisonneuvei</i> , <i>Acacia incurvaneura</i> and <i>Acacia caesaneura</i>	14	12 - 40+	02, 06, 17, 23
15	124.2703	-29.2568	1 - 6	N/A	<i>T. desertorum</i>	<i>A. maisonneuvei</i> , <i>Leptospermum</i> sp., <i>G. didymobotrya</i>	40+	40+	07, 11, 18, 27, 31, 36
20	123.9806	-29.2432	1 - 5	N/A	<i>T. desertorum</i> and <i>T. basedowii</i>	<i>T. biseriata</i> , <i>A. maisonneuvei</i>	38+	10 - 40+	13, 33, 34
21	124.4437	-29.2491	1 - 6	January 2004	<i>T. desertorum</i>	<i>T. biseriata</i> , <i>A. maisonneuvei</i> , <i>Dodonaea viscosa</i>	32+	13 - 40+	19, 24
22	124.4340	-29.2473	1 - 6	N/A	<i>T. desertorum</i>	<i>Baeckea</i> sp. GVD, <i>A. maisonneuvei</i>	40+	40+	42
23	124.1809	-29.2558	1 - 6	N/A	<i>T. basedowii</i> and <i>T. sp. rigidissima</i>	<i>A. desertorum</i> , <i>A. jamesiana</i>	17.5	15 - 20	38

Appendix B. Morphometric, reproductive and tracking data for nocturnally tracked individuals. Repro. = Reproductive, R = reproductively active, nR = non-reproductively active, Dev. = developed, Undev. = undeveloped, T = testes (length x width), PY = pouch young.

Tracking start	Tracking end	ID	Sex	Repro. status	Repro. notes	Weight (g)	Tail length (mm)	Head length (mm)	Short pes (mm)	Long pes (mm)	Total nights contact	Mean fixes per night	Mean emergence time	Mean nesting time
20/09/2015	23/09/2015	01	M	R	T: 11 x 9 mm	39	115	38	20	-	3.0	92	18:02:00	04:49:00
09/09/2015	12/09/2015	02	F	R	Dev. pouch	27	104	-	19	-	3.5	65	17:39:00	05:37:00
17/09/2015	20/09/2015	03	M	R	T: 10 x 7 mm	35	104	-	20	-	3.5	91	17:53:00	05:27:00
07/03/2016	09/03/2016	04	M	nR	-	32	108	32	15	20	3.0	84	18:34:00	05:11:00
10/03/2016	12/03/2016	05	F	nR	Undev. pouch	28	96	40	20	24	3.0	68	18:29:00	04:53:00
14/03/2016	16/03/2016	06	F	nR	Undev. pouch	32	91	37	20	22	3.0	87	18:19:00	05:13:00
17/03/2016	19/03/2016	07	F	nR	Undev. pouch	24	-	26	14	19	3.0	81	18:17:20	05:11:40
29/09/2016	02/10/2016	08	M	R	T: 11 x 10 mm	39	123	37	21	25	3.0	67	18:15:40	03:40:00
05/10/2016	08/10/2016	09	M	R	T: 10 x 9 mm	36	115	38	21	27	2.5	101	18:06:00	04:45:00
09/10/2016	11/10/2016	10	M	R	T: 10 x 10 mm	42	101	-	22	25	2.0	82	18:36:00	04:39:00
13/03/2017	16/03/2017	11	M	nR	T: 5 x 5 mm	32	109	37	21	25	3.5	89	18:31:40	05:17:00
17/03/2017	20/03/2017	12	M	nR	T: 6 x 8 mm	38	106	36	21	25	3.5	98	18:23:20	04:51:20
18/03/2017	22/03/2017	13	M	nR	T: 5 x 7 mm	31	108	37	22	26	4.0	78	18:26:30	05:24:30
09/10/2017	12/10/2017	16	F	R	Small PY	37	126	38	22	27	3.0	76	18:15:00	04:55:00
13/10/2017	15/10/2017	18	M	R	T: 11 x 10 mm	28	120	39	22	26	3.0	52	18:20:00	03:45:00
16/10/2017	27/10/2017	19	M	R	T: 10 x 8 mm	38	106	-	21	26	5.0	87	18:16:20	04:20:20

Appendices

05/03/2018	07/03/2018	21	F	nR	Undev. pouch	26	100	37	20	26	3.0	50	18:20:00	05:20:00
05/03/2018	08/03/2018	22	M	nR	T: 6 x 8 mm	46	114	39	22	28	3.0	70	18:27:00	05:25:00
07/03/2018	10/07/2018	24	M	nR	T: 7 x 5 mm	29	107	37	21	26	3.0	62	18:16:40	04:56:40
08/09/2018	11/09/2018	30	F	R	Dev. pouch	27	66	39	18	24	3.0	65	17:30:00	04:30:00
13/09/2018	16/09/2018	31	M	R	T: 11 x 9 mm	26	122	39	22	27	3.0	61	17:55:00	04:18:20
10/09/2018	12/09/2018	34	F	R	Dev. pouch	26	109	39	21	26	2.0	101	17:50:00	06:00:00
12/09/2018	15/09/2018	36	F	R	Small PY	28	98	-	20	25	3.0	50	17:40:00	05:05:00
14/09/2018	17/09/2018	39	M	R	T: 11 x 11 mm	42	104	43	21	24	3.0	57	17:45:00	04:35:00
Mean						33	107	37	20	25	3.1	76	18:10:19	04:55:22
St dev						6	13	3	2	2	0.6	16	00:19:05	00:33:12

Appendix C. All prey items recorded in the diet of *S. psammophila* identified morphometrically at species or genus level where possible. %FO = percentage frequency of occurrence.

Prey order / class	Identification	%FO per scat
VERTEBRATES		
Squamata	Scincidae	6.3
INVERTEBRATES		
Gastropoda	Gastropoda (unclassified)	1.0
	egg case	0.7
ARTHROPODA		
INSECTA		
Hemiptera	Hemiptera (unclassified)	2.3
	Heteroptera	1.1
	Membracid?	0.6
	Pentatomid?	0.4
Coleoptera	Coleoptera (unclassified)	14.8
	Derrmestidae?	0.5
	Coccinellidae	0.9
	Curculionidae	12.5
	Scarabaeidae	5.4
	Tenebrionidae	1.5
	Carabidae	1.5
	Larva	0.3
Orthoptera	Orthoptera (unclassified)	3.0
	<i>Acrididae</i>	1.2
Hymenoptera	<i>Bethylidae?</i>	1.4
	<i>Apoidea</i>	0.6
	Formicidae (unclassified)	29.1
	<i>Calomyrmex purpureus</i>	0.8
	<i>Camponotus</i> sp.	1.9
	<i>Camponotus aurocinctus</i>	1.4
	<i>Camponotus claripes</i>	2.3
	<i>Camponotus discors</i>	7.5
	<i>Camponotus gibbinotus</i>	2.8
	<i>Camponotus oetkeri</i>	9.0
	<i>Polyrhachis</i> sp.	1.9
	<i>Polyrhachis schweidlandi</i>	1.5
	<i>Crematogaster</i> sp.	0.4
	<i>Iridomyrmex</i> sp.	4.1
	<i>Iridomyrmex agilis</i>	0.4
	<i>Iridomyrmex bicknelli</i>	0.8

	<i>Iridomyrmex brunneus</i>	0.4
	<i>Iridomyrmex chasei</i>	3.0
	<i>Iridomyrmex exsanguis or dromus</i>	0.8
	<i>Iridomyrmex omalonotus</i>	2.2
	<i>Melophorus</i> sp.	1.9
	<i>Melophorus turneri perthensis</i>	0.8
	<i>Monomorium fieldi</i>	0.8
	<i>Monomorium sydneyense</i>	1.1
	<i>Odontomachus ruficeps</i>	0.4
	Ponerinae	0.8
	<i>Pseudoneoponera</i> sp.	0.8
	<i>Pheidole</i> sp.	0.6
	<i>Pheidole</i> sp. JDM 871	0.6
	<i>Pheidole mjobergi</i>	0.6
	<i>Rhytidoponera metallica</i>	1.1
	<i>Rhytidoponera dubia</i>	2.3
	<i>Rhytidoponera tyloxys</i>	1.5
	<i>Stigmacros</i> sp.	0.6
	<i>Stigmacros</i> sp. JDM 1045	1.1
Blattodea	Isoptera (unclassified)	9.2
	<i>Coptotermes</i> sp.	0.4
	<i>Nasutitermes</i> sp.	0.7
Diptera	Nematocera?	0.6
Neuroptera	<i>Myrmeleontidae</i>	0.6
ARACHNIDA		
Araneae	Araneae (unclassified)	10.1
Scorpiones	Scorpiones (unclassified)	1.2
MYRIAPODA		
Chilopoda	Chilopoda (unclassified)	9.5
Diplopoda	Diplopoda (unclassified)	1.5
VASCULAR PLANTS		
Vegetation	Unidentified (<i>excluded from analysis</i>)	4.7
OTHER		
Mammalian hair	Grooming hair (<i>excluded from analysis</i>)	80.9
Unidentified	Cuticle, tissue or other	65.4

Appendix D. *Sminthopsis psammophila* records ($n = 51$) used for the SDMs in Chapter 4, with author and date recorded (WGS 1984 Datum).

Longitude	Latitude	Author	Date
123.583	-29.889	Martinick, Hart and Kitchener	Jun-86
123.621	-29.920	Vimy Resources	2014 - 2015
123.636	-29.222	Gaikhorst and Lambert	2000 - 2008
123.685	-30.232	Pearson and Robinson	Jun-87
123.686	-30.463	NatureMap (from Gaikhorst and Lambert 2008)	2008
123.769	-30.022	Martinick, Hart and Kitchener	1986
123.800	-30.010	Hart	Jun-85
123.834	-29.236	Pearson	1987
123.862	-29.235	Turpin, Lloyd and Riley	Apr-15
123.908	-30.200	Gaikhorst and Lambert	2000 - 2008
123.982	-29.243	Turpin, Lloyd and Riley	Sep-16
124.004	-30.086	Gaikhorst and Lambert	2000 - 2008
124.016	-29.979	Gaikhorst and Lambert	2000 - 2008
124.051	-29.558	Gaikhorst and Lambert	2000 - 2008
124.052	-29.557	Gaikhorst and Lambert	2000 - 2008
124.058	-30.200	Gaikhorst and Lambert	2000 - 2008
124.089	-29.250	Turpin, Lloyd and Riley	Sep-16
124.094	-29.563	Turpin, Lloyd and Riley	Mar-16
124.119	-29.253	Turpin, Lloyd and Riley	Mar-16
124.147	-29.253	Turpin, Lloyd and Riley	Mar-16
124.284	-29.856	Turpin, Lloyd and Riley	Mar-16
124.305	-29.257	Turpin, Lloyd and Riley	Apr-15
124.307	-29.251	Turpin, Lloyd and Riley	Mar-16
124.320	-29.435	Turpin, Lloyd and Riley	Apr-15
124.439	-29.240	Turpin, Lloyd and Riley	Sep-16
124.443	-29.249	Turpin, Lloyd and Riley	Apr-15
124.453	-29.252	Turpin, Lloyd and Riley	Apr-15
124.493	-29.543	Turpin, Lloyd and Riley	Mar-16
124.498	-29.490	Turpin, Lloyd and Riley	Mar-16
124.527	-29.318	Turpin, Lloyd and Riley	Mar-16
124.598	-29.552	Turpin, Lloyd and Riley	Mar-16
131.540	-30.241	Kemper	Oct-87
132.117	-30.529	Moseby and Read	Jun-10
132.228	-30.961	Ward	Apr-09
132.236	-30.581	Churchill	Apr-01
132.245	-30.726	Churchill	Apr-01
132.361	-30.660	How and Bignall	Sep-09
132.439	-30.489	Moseby and Read	Apr-09
132.460	-30.828	Moseby	May-12
132.691	-30.678	How and Bignall	Sep-09
132.754	-30.773	How and Bignall	Sep-09

133.234	-30.614	Jansen	Oct-87
135.522	-32.859	Joanne, L.E.E.J.	Nov-15
135.733	-33.110	Andrews	Feb-69
135.983	-33.550	Eichner	Apr-69
136.141	-33.790	Driscoll	Jan-05
136.852	-33.256	Moseby and Read	Jan-09
136.870	-33.137	Moseby and Read	Jan-09
137.019	-33.136	McLean	Sep-11
137.070	-33.229	McLean	Aug-11
137.093	-33.325	Churchill	May-00
